Response of aquatic macroinvertebrate and aerial odonate assemblages to the removal of invasive alien trees in the Western Cape

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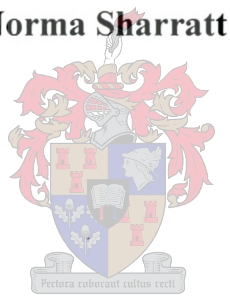

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DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not submitted it, in its entirety or in part, at any other university for a degree.

ABSTRACT

Invasive alien trees, especially *Acacia* species, are a great threat to biodiversity in South African rivers. The national Working for Water Programme is addressing the alien problem by removing alien trees from river margins. The concern is that this may be creating even further disturbance by affecting water quality and habitats. In particular, how is this affecting rare and endemic species? Benthic macroinvertebrates and aerial odonates were assessed along five Western Cape rivers in alien-invaded, cleared and natural sites between December and March. The aim was to assess the effect of both alien invasion and alien clearing on aquatic invertebrates. Odonata, being easily sampled, were also assessed as they are severely affected by the lack of understorey plants in shaded, alien-invaded sites. Odonata and benthic macroinvertebrates were treated as two separate studies and no attempt was made to correlate the results obtained from both studies. SASS5, a qualitative, rapid bioassessment technique, based on the sensitivity of the families present, was used as a measure of river health and, indirectly, of water quality. SASS indicated a decline in water quality conditions after alien clearing, a likely response to the greater insolation as well as erosion of cleared banks, resulting in elevated temperatures and suspended solids and lowered oxygen levels. Community responses to alien disturbance and other environmental factors were analysed using PRIMER and CANOCO software. Assemblages of Odonata were found to provide a rapid, cost-effective means of assessment and monitoring. Potential indicator and detector species were also identified using the Indicator Value method. Assemblage patterns of aquatic invertebrates, however, were dominated by between-river and seasonal effects. Therefore, while SASS detected overall changes in river health, without identifying the cause, potential aquatic detector taxa were identified that may be useful for linking general disturbance to alien invasion or clearing. All indicator and detector taxa identified in both studies can be used for long-term monitoring and for identifying biodiverse areas for clearing or protection. In both studies, sensitive, endemic taxa were lost after clearing, being replaced by more tolerant, widespread taxa. Recovery of the biota appears to follow the recovery succession of the vegetation, with most sensitive or endemic taxa only appearing after the recovery of indigenous plants. A number of recommendations are made regarding the restoration of both water quality (particularly with respect to shade and soil erosion) and biotope availability (particularly in terms of the recultivation of indigenous plants) in order to achieve biodiversity objectives. The role of catchment management, prioritisation procedures and long-term monitoring are also discussed.

OPSOMMING

Uitheemse, indringerbome, veral *Acacia* spesies, is 'n groot bedreiging vir biodiversiteit in Suid-Afrikaanse riviere. Die nasionale Werk vir Water-projek spreek hierdie probleem aan deur uitheemse bome van rivieroewers te verwyder. Die kommer is dat water kwaliteit en habitatte sodoende verder versteur kan word. Byvoorbeeld, hoe word endemiese en bedreigde spesies geraak? Akwatiese makroinvertebrate en volwasse Odonata in vyf Wes-Kaapse riviere is tussen Desember en Maart bestudeer en gemonster in natuurlike gebiede, in gebiede waar indringerbome teenwoordig is, en in gebiede waar hulle verwyder is. Die doel was om die effek van indringer-verwante impakte op akwatiese invertebrate vas te stel. Odonata is ook bestudeer omdat hulle maklik gemonster kan word en omdat hulle ernstig geraak word deur indringers. Die uitheemse plantegroei oorskadu die oewers en verhoed die groei van inheemse oewerplante. Die bentiese makro-invertebrate en Odonata is as twee aparte studies behandel en geen poging is gemaak om die resultate van die twee te vergelyk nie. SASS5, 'n kwalitatiewe, bioasseseringsmetode wat op die sensitiwiteit van die aanwesige families baseer word, is gebruik om waterkwaliteit op 'n indirekte manier te bepaal. SASS het aangedui dat daar 'n afname in waterkwaliteit is nadat indringerplante verwyder is. Dit is moontlik as 'n gevolg van groter blootstelling aan sonskyn en erosie van rivieroewers wat veroorsaak dat temperature en die hoeveelheid gesuspendeerde materiaal verhoog word, en dat suurstof konsentrasies verminder word. Die gevolge van indringerplante en ander omgewingsfaktore op akwatiese gemeenskappe is met PRIMER en CANOCO sagteware ontleed. Groepering van Odonata kan gebruik word om op 'n maklike en koste-effektiewe manier om die impak van indringerplante en hul verwydering te bepaal en te monitor. Aanwyserspesies is ook deur middel van die 'Indicator Value' metode geïdentifiseer. Die verspreidingspatrone van invertebraatspesies word deur geografiese en seisoenale effekte oorheers. Dus, terwyl SASS veranderinge in waterkwaliteit kan aantoon, sonder om die oorsaak daarvan te identifiseer, kan aanwyserspesies gebruik word om meer spesifieke impakte deur indringerplantegroei, of indringerverwydering, te bepaal en te monitor. Hulle kan ook gebruik word om gebiede met hoë biodiversiteit vir bewaring of indringerverwydering te identifiseer. Beide studies dui aan dat sensitiewe en endemiese taksa na indringerverwydering verlore gaan, en vervang word met meer geharde, wydverspreide taksa. Herstel van die biota volg op die herstel van die plant gemeenskappe, en die mees sensitiewe of endemiese taksa herstel eers nadat die inheemse plantegroei herstel het. 'n Aantal aanbevelings in verband met die restorasie van waterkwaliteit (veral in terme van die hoeveelheid skaduwee en erosie) en die beskikbaarheid van biotope (veral in terme van inheemse plante) om biodiversiteitsdoelwitte te bereik word gemaak. Die rol van opvanggebied bestuur, voorrang prosedures en lang termyn monitering word ook bespreek.

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Chapter 1

General Introduction

Habitat loss and invasive alien plants rank as the greatest threats to biodiversity (Allan and Flecker, 1993; Walker and Steffen, 1999; Wilcove *et al.*, 1998). The Western Cape contains the Cape Floristic Region, a global biodiversity hotspot (Myers *et al.*, 2000) that is directly threatened by invasive alien trees (Holmes, 1989). Not only a botanical hotspot, the Western Cape also has a unique and highly endemic freshwater fauna, many of which remain undescribed or undetected (Wishart *et al.*, 2003). Considered to be descendants of temperate Gondwanan fauna (Harrison, 1965), 64% of freshwater invertebrates in the Cape Floristic Region are considered endemic (Wishart and Day, 2001). These too may be affected by alien invasion, with obvious implications for management of freshwater systems. Dragonflies, in particular, are of concern as many rare and endemic species are highly threatened by alien vegetation (Samways and Taylor, 2004).

Invasion impacts directly on biodiversity by out-competing indigenous species and reducing structural diversity of the vegetation (Richardson and van Wilgen, 2004). This results, either directly or indirectly, in the demise of rare species and the displacement of indigenous species (New, 1993), thus decreasing biodiversity. Ultimately, this affects the structure and function of the ecosystem and its associated ecosystem services (Usher, 1988). Over 161 alien plants have become invasive in South Africa. These plants cover 10% of the country and the problem is growing exponentially (Department of Water Affairs and Forestry, 2003). It is estimated that, left uncontrolled, the problem will double within 15 years (Department of Water Affairs and Forestry, 2003).

Economic and hydrological impacts of invasive alien trees are fairly well documented, but there has been little research on the ecological impacts on indigenous aquatic invertebrates. In

terrestrial ecosystems, invertebrate species richness and diversity are generally lower in alien vegetation than in indigenous vegetation (Donnelly and Giliomee, 1985; Samways and Moore, 1991; Samways *et al.*, 1996).

Healthy riparian vegetation plays an important role in maintaining faunal richness (Ormerod *et al.*, 1993, Roque *et al.*, 2003) and may provide migration corridors for the maintenance of certain species or habitats for feeding and breeding. It also regulates the quality of the water by trapping sediment and nutrients, by providing shade to stabilise temperatures and reduce algal growth, by providing food through allochthonous input of litter; by stabilising banks to prevent erosion and by decreasing discharge, thus reducing downstream flooding (Vannote *et al.*, 1980; Allan and Flecker, 1993; Luger, 1998; King *et al.*, 2003).

Dense stands of invasive trees along river margins cause changes in habitat structure, fire regimes, hydrology (e.g. reduced flow, intensified flooding and channel modification) and water quality. Water quality changes may involve changes in light regime, temperature and oxygen as a result of shading by alien trees, changes in the patterns of allochthonous input of leaf litter, changes in nutrient cycling, pH and turbidity and increased erosion and sedimentation (Rutt *et al.*, 1989; Davies and Day, 1998; Maridet *et al.*, 1998). Nitrogen-fixing *Acacia* trees increase soil organic content, nitrogen, magnesium and phosphorus levels in the nutrient-poor Western Cape soils (Stock and Allsop, 1992) and increased erosion of invaded riverbanks may thus affect water chemistry. Alien trees, especially *Acacia mearnsii* De Willd. and *A. longifolia* (Andr.) Willd., have dense canopies that shade out habitats and prevent the growth of understorey plants such as sedges, reeds and grasses (Kinvig and Samways, 2000; Samways *et al.*, 1996), thus altering the availability and quality of marginal habitats. Marginal vegetation may be used by benthic larvae for nursery areas, food or protection and by adults for perch or oviposition sites. The alien trees may also present a physical barrier to movement, impeding the flight path of newly-emerged adults (Samways *et al.*, 1996).

Alien riparian vegetation therefore affects both water quality and riparian and aquatic habitats, thus disrupting ecological communities and, ultimately, affecting ecosystem structure and function. The systematic removal of alien vegetation is being conducted by the national Working for Water Programme and is expected to considerably increase the long-term survival of rare and endemic species. This public works programme, launched in 1995, is an attempt to eradicate alien vegetation and address unemployment. The programme aims to enhance water security, improve ecological integrity and biodiversity, restore the productive potential of land and invest in the marginalised sectors of South African society (Department of Water Affairs and Forestry, 2003). Riverine trees, such as alien *Acacia* species, are initially cleared by felling and burning, while follow-up treatments employ herbicides and burning to prevent resprouting.

This, in itself, is a further disturbance to the river system, as it once again causes major changes to water quality and instream and riparian habitats. Removal of riparian vegetation reduces the amount of organic inputs via leaf litter, branches or twigs, as well as fine particulate organic matter and dissolved organic matter (Bunn *et al.*, 1999). There is also a dramatic reduction in shade, resulting in increasing water temperatures, which reduces the solubility of oxygen. It is thought that temperature changes are less important than the rate of change, with sudden changes, as is experienced during alien clearing, having a significant effect on the biota (Weeks *et al.*, 1996). Temperatures will also fluctuate more widely after alien removal (Allan and Flecker, 1993). Greater exposure to sunlight results in the growth of macrophytes and filamentous algae, which are less palatable to herbivores (Bunn *et al.*, 1999). Removal of riparian vegetation also leads to increased runoff from catchments, resulting in increased salinity and nutrient loading. Bank stability is decreased, resulting in increased erosion, increased sediment and suspended solid loads, accompanied by increased turbidity. In addition to water quality changes, there may be a loss of instream habitat or a decline in habitat quality as a result of changes in flow regime, substrate modification or vegetational changes (Vuori and Joensuu, 1996).

It is likely, therefore, that alien clearing will, either directly or indirectly, affect benthic macroinvertebrate communities. No previous research has been done to determine this effect. In terms of biodiversity and ecological integrity, is the Working for Water alien clearing programme initiating recovery or is it, in fact, causing further disturbance?

Successful removal of invasive alien plants along rivers and the subsequent rehabilitation of indigenous vegetation could result in increased biological diversity as well as increased availability and sustainability of the country's water resources. It is, however, imperative that the process itself does not cause the loss of endemic or rare species that are of conservation importance.

This study aimed to assess, not only the effects of alien invasion, but also the effectiveness of the Working for Water Programme in terms of biodiversity criteria. To this end, two parallel studies were conducted, using aquatic benthic macroinvertebrates on the one hand, and aerial odonates on the other. Both have been used as ecological indicators because of their sensitivity to disturbance and their reliable reflection of environmental condition and ecological integrity. In South Africa, benthic macroinvertebrates have been used for rapid bioassessment of river health and, indirectly, water quality, using the South African Scoring System (SASS) (Chutter, 1998, Dickens and Graham, 2002), while Odonata have been used to assess biotope quality (e.g. Clark and Samways, 1996; Stewart and Samways, 1998). Although this study was essentially to assess the effects of alien disturbance on aquatic invertebrates, adult odonates were additionally assessed because many rare and endemic species are severely threatened by invasive alien trees (Samways and Taylor, 2004). Moreover, their highly conspicuous presence throughout summer, together with their ease of identification, presented a good opportunity to assess the response of aerial adults. The Final Discussion searches for common threads in the aquatic study on the one hand and the aerial study on the other and leads into management recommendations.

For both benthic macroinvertebrates and aerial odonates, an attempt was made to determine the requirements for rehabilitation and to make recommendations on how to manage the process according to biodiversity criteria. This information would provide useful baseline data for follow-on studies that could potentially address issues such as the rate of recovery under different scenarios. An attempt was also made to identify potential indicator or detector species that could be used to monitor the recovery or deterioration of sites. The results contribute to the requirements of the Convention on Biological Diversity (1992) to identify components of biological diversity important for long-term conservation, including research on indicator species.

References

Allan, J.D., Flecker, A.S. 1993. Biodiversity conservation in running waters. BioScience 43(1), 32-43.

Bunn, S.E., Davies, P.M., Mosisch, T.D., 1999. Ecosystem measures of river health and their response to riparian and catchment degradation. Freshwater Biology, 41, 333-345.

Chutter F.M., 1998. Research on the Rapid Biological Assessment of Water Quality Impacts in Streams and Rivers. Report to the Water Research Commission, Pretoria. WRC Report No. 422/1/98.

Clark, T.E., Samways, M.J., 1996. Dragonflies (Odonata) as indicators of biotope quality in the Kruger National Park, South Africa. Journal of Applied Ecology 33, 1001-1012.

Davies, B., Day, J., 1998. Vanishing Waters. University of Cape Town Press, Cape Town.

Dickens, C.W.S., Graham, P.M., 2002. The South African Scoring System (SASS) version 5 rapid bioassessment system for rivers. African Journal of Aquatic Science 27, 1-10.

Department of Water Affairs and Forestry, 2003. The Environmental Impacts of Invading Alien Plants in South Africa. Working for Water, Cape Town.

Donnelly, D., Giliomee, J.H., 1985. Community structure of epigaeic ants in a pine plantation and newly burnt fynbos. Journal of the entomological Society of southern Africa 48, 259-265.

Harrison, A.D., 1965. Geographical distribution of riverine invertebrates in southern Africa. Archiv für Hydrobiologie 61, 387-394.

Holmes, P.M., 1989. Decay rates in buried alien *Acacia* seed populations of different density. South African Journal of Botany 55(3), 299-303.

King, J.M., Scheepers, A.C.T., Fisher, R.C., Reinecke, M.K., Smith, L.B., 2003. River rehabilitation: literature review, case studies and emerging principles. WRC Report No. 1161/1/03. Water Research Commission, Pretoria.

Kinvig, R.G., Samways, M.J., 2000. Conserving dragonflies (Odonata) along streams running through commercial forestry. Odonatologica 29(3), 195-208.

Luger, M.K., 1998. Environmentally sensitive management: assessment and mitigation of impacts on urban rivers. MSc. thesis, University of Cape Town, Cape Town.

Maridet, L., Wasson, J.G., Philippe, M., Amoros, C., Naiman, R.J., 1998. Trophic structure of three streams with contrasting riparian vegetation and geomorphology. Archiv für Hydrobiologie 144, 61-85.

Myers, N., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853-858.

New, T.R., 1993. Effects of exotic species on Australian native species. In Perspectives on Insect Conservation, eds. K.J. Gaston, T.R. New, M.J. Samways, pp. 155-170. Intercept, Andover.

Ormerod, S.J., Rundle, S.D., Clare, E., Duglas, A., 1993. The influence of riparian management on the habitat structure and macroinvertebrate communities of upland streams draining plantation forests. Journal of Applied Ecology 30, 13-24.

Richardson, D.M., van Wilgen, B.W., 2004. Invasive alien plants in South Africa: how well do we understand the ecological impacts? South African Journal of Science 100, 45-52.

Roque, F.O., Trivinho-Strixino, S., Strixino, G., Agostinho, R.C., Fogo, J.C., 2003. Benthic macroinvertebrates in streams of the Jaragua State Park (Southeast of Brazil) considering multiple spatial scales. Journal of Insect Conservation 7, 63-72.

Rutt, G.P., Weatherley, N.S., Ormerod, S.J., 1989. Microhabitat availability in Welsh moorland and forest streams as a determinant of macroinvertebrate distribution. Freshwater Biology 22, 247-261.

Samways, M.J., Caldwell, P.M., Osborn, R., 1996. Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. Agriculture, Ecosystems and Environment 59, 19-32.

Samways, M.J., Moore, S.D., 1991. Influence of exotic conifer patches on grasshopper (Orthoptera) assemblages in a grassland matrix at a recreational resort, Natal, South Africa. Biological Conservation 57, 117-157.

Samways, M.J., Taylor, S., 2004. Impacts of invasive alien plants on Red-Listed South African dragonflies (Odonata). South African Journal of Science 100, 78-80.

Stewart, D.A.B., Samways, M.J., 1998 Conserving dragonfly (Odonata) assemblages relative to river dynamics in an African savanna game reserve. Conservation Biology 12(3), 683-692.

Stock, W.D., Allsop, N., 1992. Functional perspectives of ecosystems. In The Ecology of Fynbos. Nutrients, Fire and Diversity, ed. R.M. Cowling, pp. 241-259. Oxford University Press, Cape Town.

Usher, M.B., 1988. Biological invasions of nature reserves: a search for generalizations. Biological Conservation 44, 119-135.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Science 37, 130-137.

Vuori, K. Joensuu, I. 1996. Impact of forest drainage on the macroinvertebrates of a small boreal headwater stream: do buffer zones protect lotic biodiversity? Biological Conservation 77, 87-95.

Walker, B.M., Steffen, W.L., 1999. Interactive and integrated effects of global change on terrestrial ecosystems. In The Terrestrial Biosphere and Global Change: Implications for Natural and Managed Ecosystems, eds. B. Walker, W.L. Steffen, J. Canadell, J. Ingram, pp 329-375. International Geosphere Program Book Series 4, Cambridge University Press, Cambridge.

Weeks, D.C., O'Keeffe, J.H., Fourie, A., Davies, B.R., 1996. A pre-impoundment study of the Sabie-Sand river system, Mpumalanga, with special reference to predicted impacts on the Kruger National Park. Volume 1, WRC Report No. 294/1/96. Water Research Commission, Pretoria.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. BioScience 48, 607-615.

Wishart, M.J., Davies, B.R., Stewart, B.A., Hughes, J.M., 2003. Examining Catchments as Functional Units for the Conservation of Riverine Biota and Maintenance of Biodiversity. WRC Report No. 975/1/02. Water Research Commission, Pretoria.

Wishart, M.J., Day, J.A., 2001. Endemism in the freshwater fauna of the South-Western Cape, South Africa. Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie 2001.

Chapter 2

Response of aerial odonate assemblages to the removal of invasive alien trees along rivers in the Western Cape

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Abstract

Invasive alien trees, especially *Acacia* species, are a great threat to biodiversity in South African rivers. Odonata are severely affected as the trees shade the river and prevent the growth of understorey plants (reeds and grasses) used by the Odonata for perch and oviposition sites. The national Working for Water Programme is addressing the alien plant problem by removing the trees from river margins. The concern is that this may be creating even further disturbance by affecting water quality and biotope availability. In particular, how is this affecting rare and endemic species? Adult Odonata were visually assessed along five Western Cape rivers in alien-invaded, cleared and natural sites between December 2003 and May 2004. PRIMER and CANOCO software was used to analyse species abundance, diversity and assemblage patterns and to determine which environmental variables influenced these patterns. The Indicator Value method revealed that *Allocnemis leucosticta* and *Pseudagrion furcigerum* are potential indicator and detector species that could be used for monitoring purposes and management decisions. Recovery of the odonate assemblage was fairly rapid, even in only partially cleared sites. Species richness and abundance of cleared sites matched those of natural sites. Assemblage patterns reflected the vegetational succession that accompanied recovery. Recovery can therefore be gauged by species assemblages. Adult Odonata can therefore provide a rapid, cost-effective means of assessing alien disturbance and recovery, and prioritising areas for biodiversity conservation. Canopy cover, exposed soil and suspended solids were the most important environmental variables, indicating the importance of shade, marginal vegetation and anti-erosion measures. Eurytopic widespread species were the main beneficiaries of clearing. Stenotopic endemic species only appeared when the indigenous vegetation recovered. Alien clearing programs should therefore change the emphasis from clearing to restoration, assessment and protection to meet biodiversity objectives. A number of recommendations are made in this regard.

Keywords: Odonata; Alien trees; Alien removal; Rehabilitation; Rivers; Biodiversity; Conservation; Endemic species; Ecological monitoring; Riparian vegetation; Western Cape; South Africa.

1. Introduction

Invasive alien plants, along with habitat loss, rank as the greatest threats to biodiversity in South African rivers (Allan and Flecker, 1993; Walker and Steffen, 1999; Wilcove *et al.*, 1998). Dragonflies are particularly vulnerable, as they are relatively sensitive to disturbance and many rare and endemic species are highly threatened by alien vegetation (Samways and Taylor 2004). Of the 31 endemic dragonfly species in South Africa, ten are globally Red Listed species and the greatest threat is from invasive alien trees (Samways and Taylor, 2004). These threatened species occur mostly in mountainous regions of the Western Cape (Steytler, 1994; Samways and Taylor, 2004), a region considered to be a centre of endemism for Odonata (Samways, 1991; Steytler, 1994; Oelofse, 1996) as well as for a range of other fauna (e.g. Siegfried and Brown, 1992; Lombard, 1995).

Invasion impacts directly on biodiversity by out-competing indigenous species and reducing structural diversity of the vegetation (Richardson and van Wilgen, 2004). This results, either directly or indirectly, in the demise of rare species and the displacement of indigenous species (New, 1993). Ultimately, this affects the structure and function of the ecosystem and its associated ecosystem services (Usher, 1988).

Dragonflies are particularly sensitive to sun and shade conditions (e.g. Osborn, 1995; Clark and Samways, 1996; Samways and Steytler, 1996; Samways *et al.*, 1996). Many species rely on sunlit perches or basking sites to maintain their body temperatures, this behaviour allowing them to optimise activity patterns and to remain active for longer (McGeoch and Samways, 1991; Osborn, 1995). Alien trees, especially *Acacia mearnsii* De Willd. and *A. longifolia* (Andr.) Willd., have dense canopies that shade out habitats, thus reducing the number of biotopes available for sun-loving species. They also prevent the growth of understorey plants such as sedges, reeds and grasses (Kinvig and Samways, 2000) and therefore reduce the number of perch sites for territorial

adult males and oviposition sites for females. The alien trees may also present a physical barrier to movement, impeding the flight path of newly-emerged dragonflies as they leave river margins to find suitable habitats in which to mature and breed. Those most likely to be affected are endemic species that have specific habitat requirements. In fact, Samways *et al.* (2004) report that some endemic species have undergone geographical range constrictions.

The systematic removal of alien vegetation by the national Working for Water Programme is expected to considerably increase the long-term survival of rare and endemic dragonfly species. Riverine trees, such as alien *Acacia* species, are initially cleared by felling and burning, while follow-up treatments use herbicides and burning to prevent resprouting. This, in itself, is a further disturbance to the river system as it once again causes major changes in shade, temperature, erosion, turbidity, plant debris, discharge, flow and the availability of perch and oviposition sites for dragonflies. No previous research has been done to determine the effect of these methods on invertebrate communities. In terms of biodiversity and ecological integrity, is the Working for Water alien clearing programme initiating recovery or is it, in fact, causing further disturbance?

Initial indications are that recovery is fairly rapid for Odonata (Samways, 1989) as they are highly vagile (Corbet, 1999) and most species are sun-loving, therefore being attracted to newly sunlit conditions (Kinvig and Samways, 2002). Preliminary evidence of recovery exists with the rediscovery of *Proischnura polychromatica* (Barnard, 1937), *Pseudagrion newtoni* (Pinhey, 1962) and *Metacnemis angusta* (Sélys, 1863) at river margins that had been cleared (Samways *et al.*, 2004). These endemic damselflies were previously thought of as possibly extinct, having not been seen for several decades.

This study aims to assess, not only the effects of alien invasion along riparian corridors, but also the effectiveness of the Working for Water Programme in terms of biodiversity conservation of Odonata. An attempt will be made to determine the requirements for rehabilitation of cleared river

margins and to make recommendations on how Working for Water can manage the process according to biodiversity criteria. An attempt will also be made to identify potential indicator or detector species that could be used to monitor the recovery or deterioration of sites.

1.1. Odonata as bioindicators

Because it is time-consuming, expensive and logistically impractical to monitor river condition using species inventories, indicator species or species assemblages are often used to characterise the response of a river to disturbance (Kremen *et al.*, 1993). The use of either ecological or biological indicators is termed bioassessment. Indicator taxa should respond readily to environmental changes in ways that are easily measured (Kremen *et al.*, 1993). Bioassessment is often regarded as being a more sensitive and reliable measure of environmental conditions than either physical or chemical measurements (Warren, 1971). Invertebrates are commonly used as indicators because of their ubiquity, abundance, diversity, rapid generation times, mobility and functional importance in the ecosystem (McGeoch, 2002).

There is currently much debate about the definition of the term 'indicator' and what exactly an indicator should indicate (Simberloff, 1998). In general, an indicator should reflect some aspect of the environment in which it is found (McGeoch, 2002). Indicator species include characteristic species (Dufrêne and Legendre, 1997) that are not only specific to a habitat state but have a high probability of being sampled in that habitat (i.e. high fidelity and specificity). Therefore, in restored rivers, the appearance of an indicator species characteristic of natural, undisturbed sites (i.e. indigenous riparian vegetation) would indicate successful restoration.

Species may also be classified as detector species (Jenkins, 1971) if they have medium fidelity and medium specificity, so detect not only changes, but also the direction of those changes (McGeoch *et al.*, 2002). Thus, a decline in abundance of detector species may indicate increased disturbance (i.e. alien invasion), while an increased abundance would indicate recovery. Detector

species are useful for longer-term monitoring within and across ecological states and determine directional changes, while indicator species can only be sampled in undisturbed or healthy conditions. Therefore, the information they provide are complementary to each other.

The Odonata have considerable potential as indicators (Kremen *et al.*, 1993; Samways, 1993a; Hawking and New, 2003). They are conspicuous, taxonomically well known and easily identified in the field (using binoculars), so counts are quick and cost-effective (Moore, 1997). They occupy a wide range of aquatic habitats and have been observed to respond rapidly to changes in physical conditions (McGeoch and Samways, 1991; Samways, 1989, 1993b). Brown (1991) ranked indicator taxa according to their suitability and, according to his classification, the Odonata ranked in the top 20%.

Odonates also tend to be biotope specific (Schmidt, 1985; Castella, 1987; Clark, 1991) and their response to disturbance is well defined: they replace or are replaced by other species (Clark and Samways 1996). Thus, generalists replace specialists in disturbed environments. Assemblages of Odonata species can therefore be used to classify sites. In 1985, Schmidt introduced the concept of RSO, or Representative Spectrum of Odonata, to classify biotopes. He suggested that human disturbance usually led to a change in relative abundances of Odonata species, followed by the disappearance of certain more sensitive species. Species with more specific biotope preferences are more susceptible. Moreover, changes in the RSO would reflect the nature of the disturbance. These changes could form the basis of management decisions. Several studies have subsequently classified biotopes according to species assemblages of Odonata for the purpose of assessing biotope quality (e.g. Chovanec and Waringer, 2001; Clark and Samways, 1996, Stewart and Samways, 1998, Bulánková, 1997). The presence or absence of certain species will thus mirror both human disturbances and physical aspects of the biotope (e.g. water regime or vegetation).

Odonate larvae are used in the assessment of water quality (e.g. in SASS5, Dickens and Graham, 2002) so the adults relate to both water conditions and landscape patterns (Samways, 1993a). Odonata are also considered to be excellent umbrellas, representing land areas and faunas in biodiversity conservation (Samways, 1993a) and are therefore often used for partial selection of reserve sites (Prendergast *et al.*, 1993). Finally, as many Odonata are of conservation importance, they can assist in making conservation decisions regarding endemism or rarity.

2. Methods

2.1. Study Area

The Western Cape is home to the Cape Floristic Region, an internationally recognised biodiversity hotspot (Myers *et al.*, 2000). The aquatic invertebrates of this region exhibit a high degree of endemism, a combined product of climatic, geological, geomorphological and vegetation characteristics (Harrison and Agnew, 1962). Vegetation typically found in the upper catchments comprises sclerophyllous fynbos. The region has a mediterranean climate with hot, dry summers and cool, rainy winters. Water flowing over the quartzitic sandstone of the mountains, which form part of the Table Mountain Group (Vegter, 1995), is characteristically acidic and low in nutrients and dissolved solids, the latter consisting predominantly of sodium and chloride (Day and King, 1995).

Study sites were located along five rivers that had had alien vegetation removed from sections of their riparian zones over the past two years. These were the Molenaars, the Holsloot, the Rondegat, the Witte and the Dwars Rivers (Fig. 1). While the Rondegat River forms part of the Olifants River catchment, the other four rivers form part of the Breede River catchment. Along each river, three disturbance regimes were identified: natural (indigenous riparian vegetation), alien (invasive alien trees, generally *Acacia mearnsii*) and cleared (alien trees removed). Five or six sites of each regime were selected for each river (i.e. 15 sites per river). Sites were 15 m long

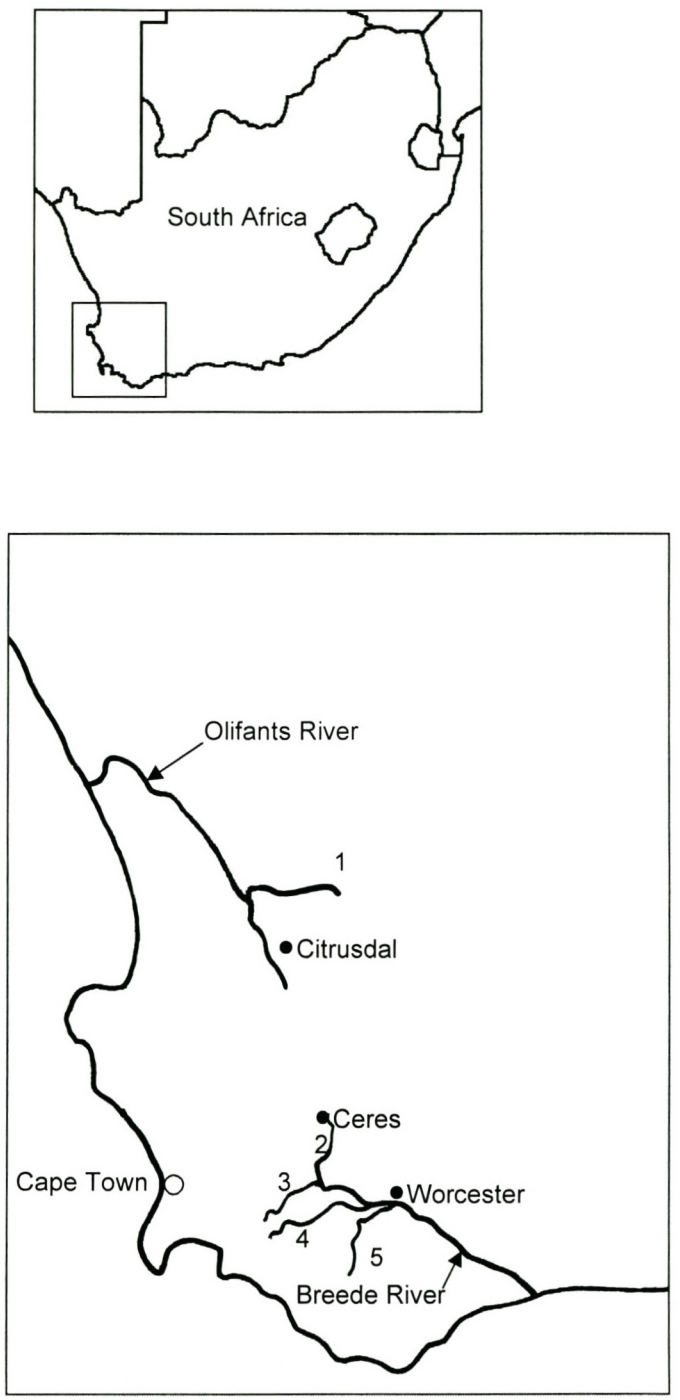


Fig. 1. Location of the five Western Cape rivers studied. 1 = Rondegat River, 2 = Dwars River, 3 = Witte River, 4 = Molenaars River, 5 = Holsloot River.

and were spaced at intervals of about 20 m. Sampling was conducted monthly between December 2003 and May 2004, generating a total of 25 alien, 28 cleared and 25 natural samples per month. For comparative purposes, all sites were located in the middle reaches of the rivers.

Cleared sites varied in terms of the density of the original alien invasion and the extent of recovery. Vegetation in cleared sites along the Dwars and Witte Rivers consisted predominantly of grass, while many Molenaars, Holsloot and Rondegat cleared sites had high proportions of palmiet reed, *Prionium serratum* L.f. ('*Prionium*') or short indigenous bushes. Certain cleared sites along the Rondegat River were sparsely vegetated and the banks were very exposed.

Most natural sites had indigenous riparian thicket consisting mostly of *Brabejum stellatifolium* L. and *Metrosideros angustifolia* [L.] Smith. For the sake of clarity, these tree species were referred to as 'tall indigenous trees' to distinguish them from shorter indigenous bushes. Shading by these trees limited understorey growth of *Prionium* and grass, although a recent fire in natural sites along the Rondegat River resulted in an increase in *Prionium* and short fynbos elements. The natural sites along the Witte River had actually been cleared in 1998 and had probably not recovered to 'climax' stage yet. They were therefore referred to as 'near-natural'. Here, the dominant vegetation type was *Prionium*, with short indigenous bushes also being present. Natural sites were absent from the Dwars River and this river was therefore excluded from analyses of pooled data.

Alien sites varied in the density of alien invasion and, therefore, in factors such as shade, bank exposure and the presence of grass, *Prionium* and sedges. Alien sites along the Molenaars and Witte Rivers had dense stands of *A. mearnsii* with over 70% canopy cover and shade. The Holsloot alien sites had been partially cleared on one bank only and were therefore more open and exposed with 30-50% canopy cover. Similarly, the Dwars River alien sites had wide cobbled floodplain areas separating the alien trees from the water's edge, thus reducing canopy cover,

allowing more exposure to sunlight and, hence, increased growth of grasses and *P. serratum*. Alien trees were generally *A. mearnsii* and, to a lesser extent, *A. longifolia*, although *Eucalyptus camaldulensis* Dehnh. occurred amongst the *Acacia* along the Rondegat and Dwars Rivers.

2.2. Sampling methods

Adult Odonata were counted and identified to species level. Because females and tenerals are not consistently associated with water (Samways *et al.,* 1996), only adult males were counted as they set up territories at oviposition sites, thus matching dragonfly species with particular biotopes (Clark and Samways, 1996). Initially, voucher specimens were collected to confirm species identifications using keys (Pinhey, 1951, 1984, 1985; Tarboton and Tarboton, 2002). Thereafter a pair of close-focus binoculars were used to aid visual identification, assisted by a field guide (Tarboton and Tarboton, 2002). *Trithemis furva* Karsch and *T. dorsalis* (Rambur) are indistinguishable in the field and were therefore grouped together as *Trithemis furva/dorsalis*. However, subsequent identifications suggest that they were probably all *T. furva*. Odonata assemblages were visually assessed along both banks (including the stream margin 2 m from the stream edge) and across the river itself, for a minimum of 10 min. Visual surveys were conducted on fine, windless days between 11h00 and 15h00 to ensure maximum activity. Moore (1991) considered this method of sampling to be about 100% accurate for Anisoptera and 80% accurate for Zygoptera, which are less conspicuous.

Riparian vegetation was classified into broad categories. These were: alien *Acacia* spp., alien *Eucalyptus* spp., tall indigenous trees (mostly *M. angustifolia* and *B. stellatifolium*), grass (which included sedge), *Prionium* and short indigenous vegetation (including ericoid and proteoid fynbos shrubs, such as *Erica caffra* L. and *Brachylaena neriifolia* [L.f.] R. Br.).

At each site, the following environmental variables were measured:

- river system (in order of increasing latitude: 1 = Rondegat, 2 = Witte, 3 = Molenaars, 4 = Holsloot. All rivers were less than 17' apart within the 19° longitude.)
- disturbance regime (1 = natural, 2 = near-natural, 3 = cleared, 4 = alien, 5 = dense alien)
- dissolved oxygen, temperature, pH and electrical conductivity (YSI 556MPS)
- flow (time taken for a floating object to be carried five metres)
- mean width and depth of river
- percentage of cobbles, gravel and sand in the river substrate
- percentage cover of each vegetation category given above (in a 3 m marginal recording zone)
- percentage cover of exposed rocks in the river (usable as perch sites)
- percentage cover of exposed soil on the banks (in a 1 m marginal recording zone)
- percentage shading of the river by riparian vegetation (100 - % sky in the canopy over the water)
- percentage canopy cover (percentage of river covered by trees)
- total suspended solids (TSS). (River water was collected from high-flow areas and filtered through preweighed 45μm GF/F filters within 24 hr of sampling. The filters were oven-dried at 40˚C for 24 hr, reweighed and the difference calculated.)
- percentage of the water surface with riffles (broken flow) and pools (no visible flow) present

2.3. Data analyses

Mean abundance and species richness were calculated for alien, cleared and natural sites in all five rivers. In addition, average taxonomic distinctness (Clarke and Warwick, 2001a) was calculated using PRIMER V5 software. Average taxonomic distinctness (Δ^*) has been proposed as a biodiversity measure and calculates the average taxonomic distance between any two species chosen at random from a sample (Clarke and Warwick, 2001b). Analysis of variance and student's *t*-test were used to analyse for differences between means.

For all subsequent analyses, data collected from the Molenaars, Rondegat, Witte and Holsloot Rivers were pooled and averaged over four months (December to March). Multivariate community analysis of Odonata abundance data was made using PRIMER v5.0 software (Clarke and Warwick, 2001b). Sampling units with similar species assemblage patterns were identified and grouped together in habitat clusters. This was achieved with the CLUSTER programme within the PRIMER software package. Hierarchical agglomerative clustering was performed on Bray-Curtis similarity matrices, using group-average linking, to produce dendrograms (Bray and Curtis, 1957). The data were square-root transformed to remove heterogeneity of variance (Underwood, 1998). Non-metric multi-dimensional scaling (MDS) visually displayed the relationships between the sampling units in the ordination analysis.

The species assemblages responsible for distinguishing habitat clusters were then identified with the SIMPER (similarity percentages) routine. This examines the overall percentage contribution each species makes to the average dissimilarity between habitat clusters. The species that were listed as important in discriminating between clusters were considered to be characteristic species.

Analysis of similarity (ANOSIM – Clarke, 1993) was used to establish the significance of differences between sampling units and habitat clusters. ANOSIM is a non-parametric permutation procedure applied to the similarity matrix that underlies the ordination (Clarke and Warwick, 2001b). This method overcomes the problem of non-normal probability distributions resulting from the dominance of zero values in multispecies abundance data, which prevent the assumptions of parametric multivariate analysis of variance (MANOVA) from being satisfied (Clarke and Warwick, 2001b).

Indicator and detector Odonata species (indicator species) were identified for each habitat cluster using the indicator value (*IndVal*) method (Dufrêne and Legendre, 1997). The *IndVal* method combines the specificity of a species (uniqueness to a particular habitat type) and its fidelity

(frequency within that habitat type) (Dufrêne and Legendre, 1997). Species with both a high specificity and fidelity to a habitat type will have a high indicator value (*IndVal* - expressed as a percentage).

IndVal is calculated as follows:

Specificity $A_{ij} = Nindividuals_{ij}/Nindividuals_i$

where $Nindividuals_{ij}$ is the mean number of species *i* across sites of group *j*, and $Nindividuals_i$ is the sum of the mean numbers of individuals of species *i* over all groups.

Fidelity $B_{ij} = Nsites_{ij} /Nsites_j$

where $Nsites_{ij}$ is the number of sites in cluster (habitat) *j* where species *i* is present, and $Nsites_j$ is the total number of sites in that cluster.

The percentage indicator value for species *i* in cluster *j* is:

$IndVal_{ij} = A_{ij} x\ B_{ij} x\ 100$

The *IndVals* were calculated for each species. Dufrêne and Legendre's (1997) random reallocation procedure was used to test the significance of the *IndVal* measure for each species. Species with significant *IndVals* of greater than say 70% (subjective choice, van Rensburg *et al.*, 1999) were regarded as characteristic indicator species for that habitat. Species with medium-range *IndVal* values (e.g. 50-70%) were regarded as detector species.

To match the species abundance patterns to environmental data, the BIO-ENV procedure within the PRIMER programme was used (Clarke and Warwick, 2001b). BIO-ENV is a measure of agreement in pattern between the similarity matrix of the species abundance data and the dissimilarity matrices of the environmental data (a large number of dissimilarity matrices being

generated for each of the possible combinations of the specified environmental variables). Spearman's rank correlation coefficient was used to match the biotic and abiotic matrices. Euclidean distance was used as dissimilarity measure for the environmental matrices. The environmental variables were standardised and the percentage values were log-transformed.

However, BIO-ENV merely detects matching patterns between species and environmental data and no causal relationship can be implied (Clarke and Warwick, 2001b). Significance testing is also problematic, given the lack of model assumptions underlying the procedure. Therefore, this procedure was used merely as an exploratory tool to identify the main ecological correlates. Statistical confirmation was sought using Canonical Correspondence Analysis (CCA) (ter Braak, 1986) using CANOCO version 4.5 software (ter Braak and Smilauer, 2002). CCA adds the power of regression to the ordination (ter Braak and Verdonschot, 1995). It is a direct gradient analysis technique that uses multiple regression to select linear combinations of environmental variables that account for most of the variation in the species scores on each axis. Therefore, the ordination diagram expresses the pattern of variation in the species data, together with the main relations between the species and each environmental variable (ter Braak, 1988). The method is considered to be fairly robust, accommodating, *inter alia*, skewed species distributions, interrelated environmental variables and incomplete environmental measurements (Palmer, 1993).

However, CCA is a constrained ordination technique and, as such, only examines variation in species composition that are explicitly attributable to the supplied environmental variables (Økland, 1996). That is, variation due to environmental variables that were not measured in the study is effectively ignored. BIO-ENV, on the other hand, is an *a posteriori* assessment of correlations with existing species patterns (which may have been affected by unmeasured variables) and, as such, was appropriate as an initial assessment as unmeasured variables were accommodated.

CCA ordination diagrams were used to display the distribution patterns underlying species or sites (points) as explained by the environmental variables (arrows). These diagrams are interpreted as follows: each environmental variable is represented by an arrow, which indicates its direction of maximum variation; dropping a perpendicular from a site or species point to the arrow shows the relative position of the site or species along the environmental gradient (represented by the arrow). This provides a means of visualising the differential habitat preferences of the taxa (ter Braak and Verdonschot, 1995). The length of the arrow is a measure of how much the species relative abundances differ along that environmental gradient (i.e. the rate of change of the weighted averages). The longer arrows are therefore more important in determining species distributions. The relative magnitudes of the canonical coefficients also indicate the relative importance of each environmental variable in predicting assemblage composition.

Included as nominal variables in the CCA were 'disturbance regime' and 'river system'. For the ordination diagrams, each class (i.e. natural, near-natural, cleared, alien, dense alien, Rondegat, Witte, Molenaars, Holsloot) was converted to a dummy variable (with a value of one if present in a sample, and zero if absent) and represented as a centroid (the average scores of the samples belonging to that class).

In addition to the overall CCA, a partial ordination was performed to eliminate between-river effects. This was achieved by specifying 'river' as a co-variable. Partial ordination yields an ordination diagram of the residual variation in the species data after the covariable is factored out by multiple linnear regression (Verdonschot and ter Braak, 1994).

Forward selection was used to rank environmental variables in order of importance according to the eigenvalues produced (i.e. variation in the species data accounted for by that variable) if each variable was considered individually. Monte Carlo permutation tests (Manly, 1990; ter Braak, 1992), using 199 unrestricted random permutations, were performed to test the significance of the

environmental variables (individually and collectively) on species distribution patterns. The Monte Carlo permutation tests replace the *F*- and *t*-tests in forward selection in multiple regression.

3. Results

3.1. Species richness and abundance

A total of 23 species of Odonata were sampled (Table 1). Species richness, abundance and taxonomic distinctness differed significantly between alien disturbance regimes ($P < 0.001$). Mean abundance and species richness were greatest in cleared sites (Table 1, Fig. 2A), the latter significantly so ($P < 0.05$), while natural sites had the highest average taxonomic distinctness. Natural and cleared sites differed significantly from each other in terms of mean abundance, but not in terms of species richness and taxonomic distinctness. Alien sites had significantly lower mean species richness and average taxonomic distinctness than both cleared and natural sites ($P < 0.05$).

This pattern did not, however, hold true for all rivers. Fig. 2C and F show that the Dwars and Holsloot rivers both had the highest species richness in alien sites. Both these rivers had relatively low alien densities and the river banks were partially exposed to sunlight, resulting in growth of grasses and *P. serratum*.

Both Anisoptera and Zygoptera were most abundant in cleared sites. Of the most abundant species (contributing up to 95% of the total abundance), only *A. leucosticta* and *E. frenulata* were significantly most abundant in natural sites, while *P. kersteni*, *T. furva/dorsalis*, *O. julia capicola* and *T. arteriosa* were most abundant in cleared sites ($P < 0.05$) (Table 1).

The highest incidence of Anisoptera was encountered in cleared sites (Table 2), while the highest incidence of Zygoptera occurred in natural sites. Of the most abundant species (collectively

Table 1

Mean abundance per sample per species of Odonata sampled in natural, cleared and alien sites between December and March, arranged in descending order of total abundance. Mean abundance, species richness and average taxonomic distinctness are given for each disturbance regime. Subscripts indicate means that are significantly higher than natural ($_n$), cleared ($_c$) or alien ($_a$) means ($P < 0.05$). (* endemic to South Africa; ** endemic to the southern Cape; *** endemic to the Western Cape Province; + endemic to the Cape Province and Angola; (*R*) = Rare.)

	Natural mean ± SD n = 80	**Cleared** mean ± SD n = 116	**Alien** mean ± SD n = 104	***N*** (Total no. of individuals)
Zygoptera				
Pseudagrion kersteni (Gerstäcker, 1869)	0.03 ± 0.16	2.82 ± 4.86 $_{n,a}$	0.43 ± 0.95	374
Pseudagrion furcigerum (Rambur, 1842)***	1.54 ± 2.47 $_a$	1.22 ± 2.30 $_a$	0.25 ± 0.65	290
Elattoneura frenulata (Hagen in Sélys, 1860)+	1.60 ± 2.08 $_{c,a}$	0.69 ± 1.23 $_a$	0.10 ± 0.33	218
Chlorolestes umbratus Hagen in Sélys, 1862** *(R)*	0.73 ± 2.00 $_c$	0.03 ± 0.21	0.67 ± 2.05 $_c$	131
Allocnemis leucosticta Sélys, 1863*	0.94 ± 1.29 $_{c,a}$	0.09 ± 0.34	0.07 ± 0.29	92
Elattoneura glauca (Sélys, 1860)	0.16 ± 0.56	0.37 ± 1.37 $_n$	0.14 ± 0.46	70
Pseudagrion draconis Barnard, 1937*	0.14 ± 0.44 $_a$	0.32 ± 0.91 $_a$	0.20 ± 0.77	68
Platycypha fitzimonsi (Pinhey, 1950)	0.05 ± 0.31	0.10 ± 0.60	0.04 ± 0.24	19
Ischnura senagalensis (Rambur, 1842)	0.06 ± 0.29	0.05 ± 0.22	0.03 ± 0.17	14
Ceriagrion glabrum (Burmeister, 1839)	0	0.05 ± 0.32	0	6
TOTAL (Zygoptera)	5.25	5.74	1.93	1282

(Continued overleaf)

Table 1 continued

	Natural mean ± SD n = 80	**Cleared** mean ± SD n = 116	**Alien** mean ± SD n = 104	***N*** (Total no. of individuals)
Anisoptera				
Trithemis furva Karsch, 1899/ *dorsalis* (Rambur, 1842)	1.00 ± 1.01 $_{a}$	1.42 ± 1.05 $_{n,a}$	0.60 ± 0.81	307
Aeshna subpupillata McLachlan, 1896*	0.63 ± 0.97 $_{a}$	0.98 ± 1.34 $_{a}$	0.32 ± 0.91	197
Orthetrum julia Kirby 1900 *capicola* Kimmins, 1957**	0.36 ± 0.56	0.95 ± 1.38 $_{n,a}$	0.31 ± 0.59	171
Anax speratus Hagen, 1867	0.46 ± 0.55 $_{a}$	0.56 ± 0.53 $_{a}$	0.16 ± 0.37	119
Trithemis arteriosa (Burmeister, 1839)	0.15 ± 0.39 $_{a}$	0.59 ± 0.92 $_{n,a}$	0.30 ± 0.70	111
Paragomphus cognatus (Rambur, 1842)	0.23 ± 0.50 $_{a}$	0.24 ± 0.45 $_{a}$	0.08 ± 0.33	54
Crocothemis sanguinolenta (Burmeister, 1839)	0.16 ± 0.37 $_{a}$	0.25 ± 0.51 $_{a}$	0.02 ± 0.14	44
Zygonyx natalensis (Martin, 1900)	0.21 ± 0.52 $_{a}$	0.07 ± 0.26	0.07 ± 0.25	32
Anax imperator Leach, 1815 *mauritianus* Rambur, 1842	0.03 ± 0.16	0.10 ± 0.31	0.03 ± 0.17	17
Trithemis stictica (Burmeister, 1839)	0.09 ± 0.33 $_{a}$	0.03 ± 0.18	0	11
Tramea limbata (Desjardins, 1832)	0	0.04 ± 0.20 $_{n,a}$	0.01 ± 0.10	6
Palpopleura jucunda Rambur, 1842	0	0.05 ± 0.22 $_{n,a}$	0	6
Ceratogomphus pictus Sélys, 1854	0	0.01 ± 0.09	0	1
TOTAL (Anisoptera)	3.32	5.29	1.88	1076
Mean total abundance of Odonata per sample $F_{2, 297} = 43.4$, $P < 0.001$	**8.55** ± 1.05	**11.03** ± 1.11 $_{a,n}$	**3.81** ± 0.59	
Mean no. of Odonata species per sample $F_{2, 297} = 28.27$, $P < 0.001$	**4.66** ± 2.20 $_{a}$	**5.15** ± 2.13 $_{a}$	**2.42** ± 2.11	
Average taxonomic distinctness (Δ*) $F_{2, 297} = 14.78$, $P < 0.001$	**74.42** ± 25.82 $_{a}$	**70.92** ± 18.41 $_{a}$	**52.00** ± 43.79	
Average taxonomic distinctness (Δ*) $F_{2, 297} = 14.78$, $P < 0.001$	**74.42** ± 25.82 $_{a}$	**70.92** ± 18.41 $_{a}$	**52.00** ± 43.79	

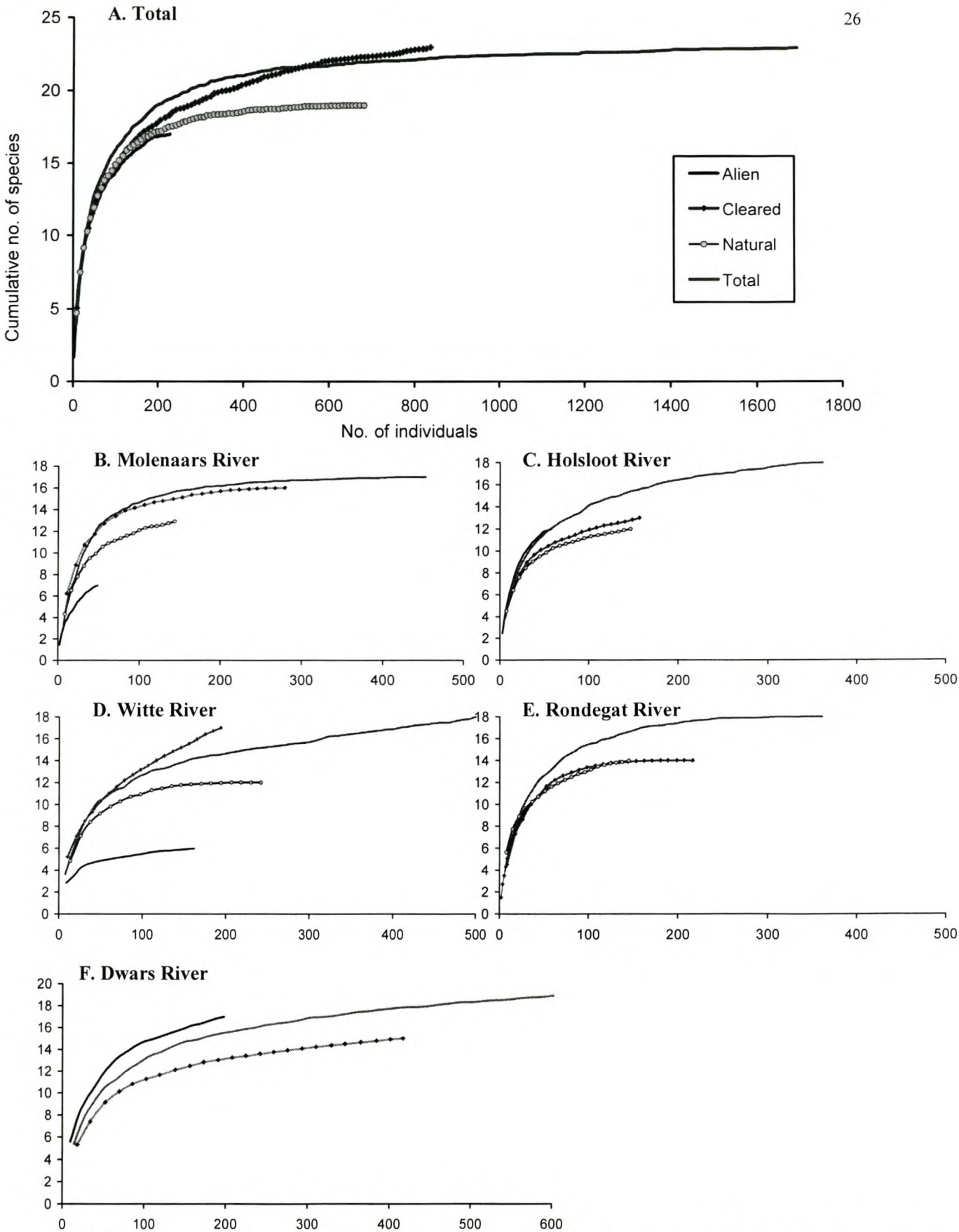


Fig. 2. Species accumulation curves for Odonata sampled from natural, cleared and alien sites in the Molenaars, Holsloot, Witte, Rondegat and Dwars Rivers between December and March. A total of 240 samples were counted (excluding the Dwars River), 60 from each river and 20 from each disturbance regime. No natural sites were sampled along the Dwars River and only 44 samples were counted here.

Table 2

Mean incidence (number of sites of occurrence) of Odonata in cleared, alien and natural sites, arranged in order of descending incidence. (* endemic to South Africa; ** endemic to the southern Cape; *** endemic to the Western Cape Province; + endemic to the Cape Province and Angola; (R) = Rare.)

	Natural mean ± SD n = 80	**Cleared** mean ± SD n = 116	**Alien** mean ± SD n = 104	**Total incidence** (Total no. of sites)	*N* (Total no. of individuals)
Zygoptera					
*Pseudagrion furcigerum****	0.5	0.54	0.2	102	290
Elattoneura frenulata+	0.6	0.4	0.08	89	218
*Allocnemis leucosticta**	**0.51**	0.05	0.04	48	92
*Chlorolestes umbratus** (R)*	0.21	0.01	0.32	45	131
Pseudagrion kersteni	0.03	0.35	0.07	37	374
*Pseudagrion draconis**	0.1	0.14	0.02	22	68
Elattoneura glauca	0.09	0.04	0.05	14	70
Platycypha fitzimonsi	0.03	0.04	0.02	7	19
Ischnura senagalensis	0.05	0.02	0.01	7	14
Ceriagrion glabrum	0	0.05	0	4	6
TOTAL	**2.12**	1.64	0.81	375	1282
Anisoptera					
Trithemis furva/ dorsalis	0.63	0.9	0.32	153	307
Anax speratus	0.44	0.57	0.12	93	119
*Orthetrum julia capicola***	0.33	0.52	0.2	87	171
*Aeshna subpupillata**	0.4	0.39	0.06	70	197
Paragomphus cognatus	0.2	0.26	0	38	54
Trithemis arteriosa	0.14	0.29	0.02	37	111
Crocothemis sanguinolenta	0.16	0.24	0.02	35	44
Zygonyx natalensis	0.16	0.08	0.04	23	32
Trithemis stictica	0.08	0.05	0	10	11
Anax imperator	0.03	0.06	0.02	9	17
Tramea limbata	0	0.06	0	5	6
Palpopleura jucunda	0	0.06	0	5	6
Ceratogomphus pictus	0	0.01	0	1	1
TOTAL	2.57	**3.49**	0.8	566	1076

contributing up to 95% of the abundance), only two zygopterans, *E. frenulata* and *A. leucosticta*, had the highest incidence (as well as abundance) in natural sites. The majority of Anisoptera species were most frequently encountered in cleared sites (Table 2), while of the zygopterans, only two species, *P. furcigerum* and *P. kersteni*, were most frequently encountered in cleared sites. The zygopteran, *C. umbratus*, was the only species with the highest incidence in alien sites, while only *P. cognatus* was completely absent from alien sites. *T. furva/dorsalis*, *A. speratus* and *O. julia capicola* appear to be relatively eurytopic, occurring relatively frequently in all disturbance regimes, while most Zygoptera had relatively high incidences in only one or two disturbance regimes.

Cluster analysis of averaged data from the Rondegat, Molenaars, Witte and Holsloot Rivers revealed clear grouping of species abundance data according to disturbance regime (Fig. 3). The cleared and natural groups were more similar to each other (70.3% similarity) than to the alien group (56.1% similarity). There was also more variability between alien sites, with only 64% similarity within the group, compared with 79% similarity within the cleared group, and 87% similarity within the natural group. Multivariate ANOSIM revealed a significant difference between all three groups at $P = 0.04$ ($R = 0.37$). Univariate ANOVA of mean abundance and species richness data also revealed a significant difference between groups ($P < 0.001$) (Table 1).

Demarcation of groups according to disturbance regime was less clear for the cluster analysis of the unaveraged total data set (Fig. 4A). ANOSIM of sites continued to yield a significant difference between alien sites and both cleared and natural sites at $P < 0.01$ ($R = 0.48$ and 0.37 respectively), but not between cleared and natural sites ($R = 0.20$). However, because of the risk of pseudoreplication from sampling sub-sites within a site (Hurlbert, 1984), ANOSIM2 (with no replication) was also performed. This confirmed a global significance at $P = 0.001$ ($R = 0.674$).

Analysis of variance of mean abundance data also revealed a significant difference between groups at $P < 0.001$ ($F_{61,1426} = 1.83$).

The first group to be separated out (dense alien), had only 24.9% similarity to all other sites and included very shaded sites with high densities of *A. mearnsii* (canopy cover >70%). At the 38.5% similarity level, a second alien group was separated from the remaining samples, this group having medium densities of aliens, reduced canopy cover (30-70%) and greater exposure to sunlight. The remaining samples were mostly cleared and natural sites. The most dissimilar sites were the near-natural sites along the Witte River (41% similarity to the remaining cleared and natural sites). The remaining cleared and natural sites formed two groups with 48.1% similarity, one consisting mostly of cleared sites and the other mostly of natural sites.

Dominant vegetation types (Fig. 4B) closely followed the disturbance types (Fig. 4A). Grass was dominant in cleared sites, *Prionium* in near-natural sites and tall indigenous trees in natural sites. However, some overlap did occur. For instance, *Prionium* was dominant in several cleared sites, as well as in near-natural sites. Relatively little *Prionium* growth occurred in natural sites. Similarly, short indigenous bushes were dominant in several cleared sites, as well as a few natural sites.

The MDS ordination of sites according to the species they contain, shows clear grouping according to disturbance regime (Fig. 5A). The similarity between cleared and natural sites is evident, as is the dissimilarity of dense alien sites to all other sites. Also evident, is the variability of the medium-dense alien sites, several of which show similarities to cleared and natural sites.

When alien and dense alien sites were excluded from the MDS ordination, sites were clearly grouped according to the dominant vegetation type they (Fig. 6). Species distribution patterns in *Prionium* and indigenous vegetation (both short and tall) were more similar to each other than to

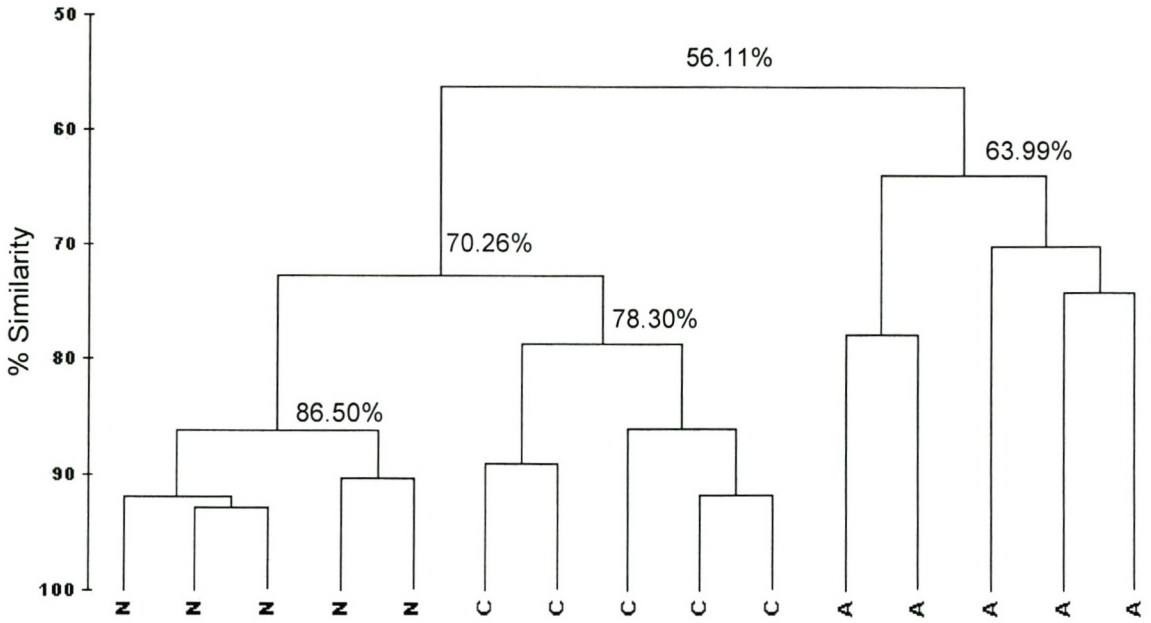


Fig. 3. CLUSTER dendrogram of Odonata species abundance data from alien (A), cleared (C) and Natural (N) sites. The dendrogram is derived from averaged, fourth-root transformed data.

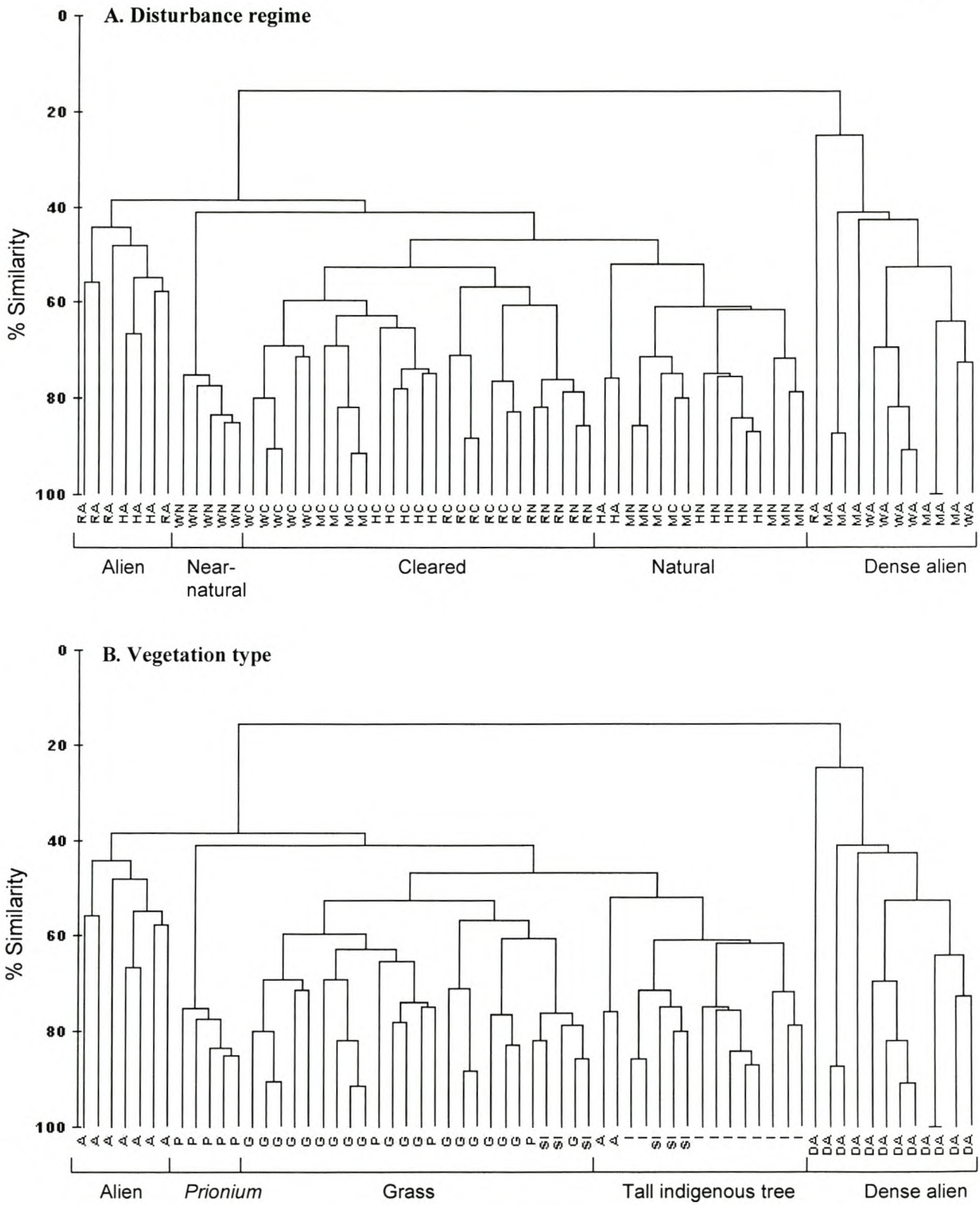
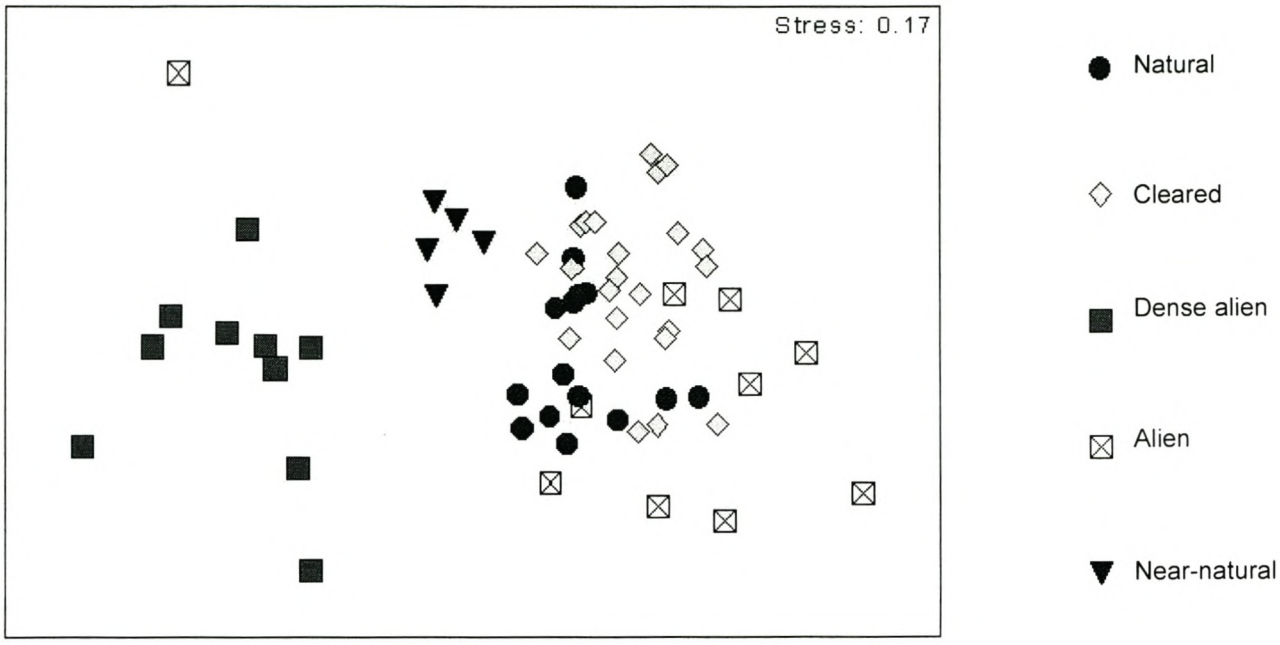


Fig. 4. Cluster analysis of Odonata species abundance data in cleared, natural and alien sites according to alien disturbance regime (A) and vegetation type (B). (M = Molenaars River, H = Holsloot River, W = Witte River, R = Rondegat River, A = Alien, N = Natural, C = Cleared, P = *Prionium*, G = Grass, I = Tall indigenous trees, SI = Short indigenous bushes, DA = Dense alien trees.)

A. Disturbance regime



B. River system

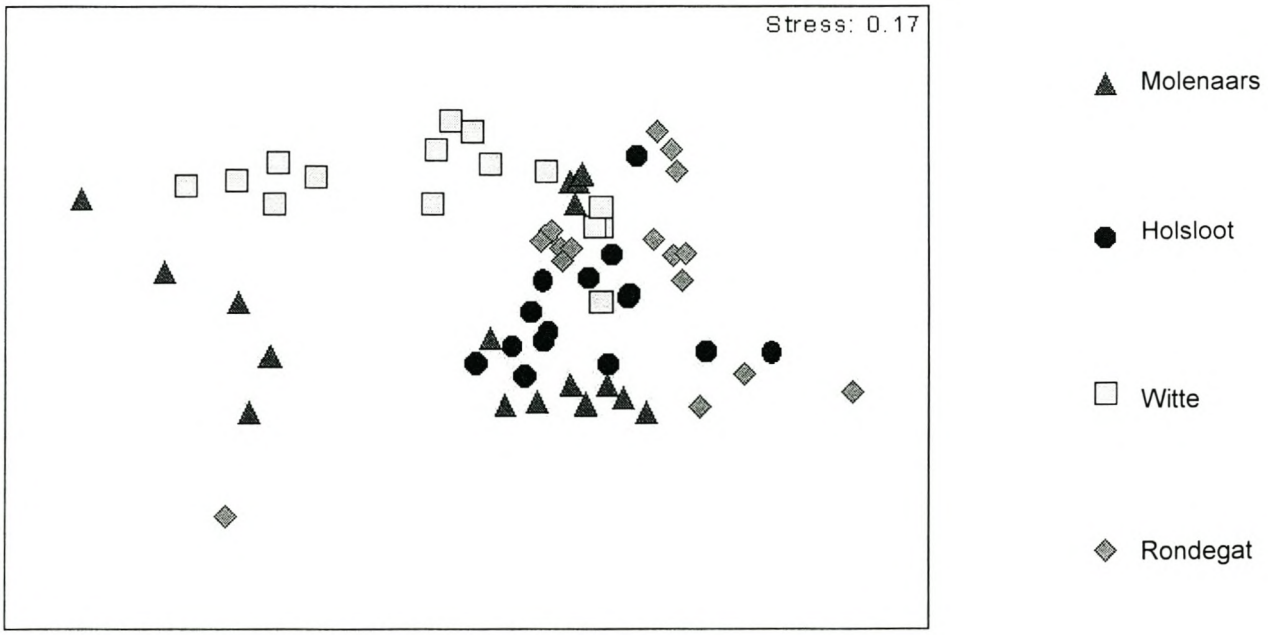


Fig. 5. MDS ordination of sites based on Odonata abundance data, showing grouping according to alien disturbance regime (A) and rivers (B).

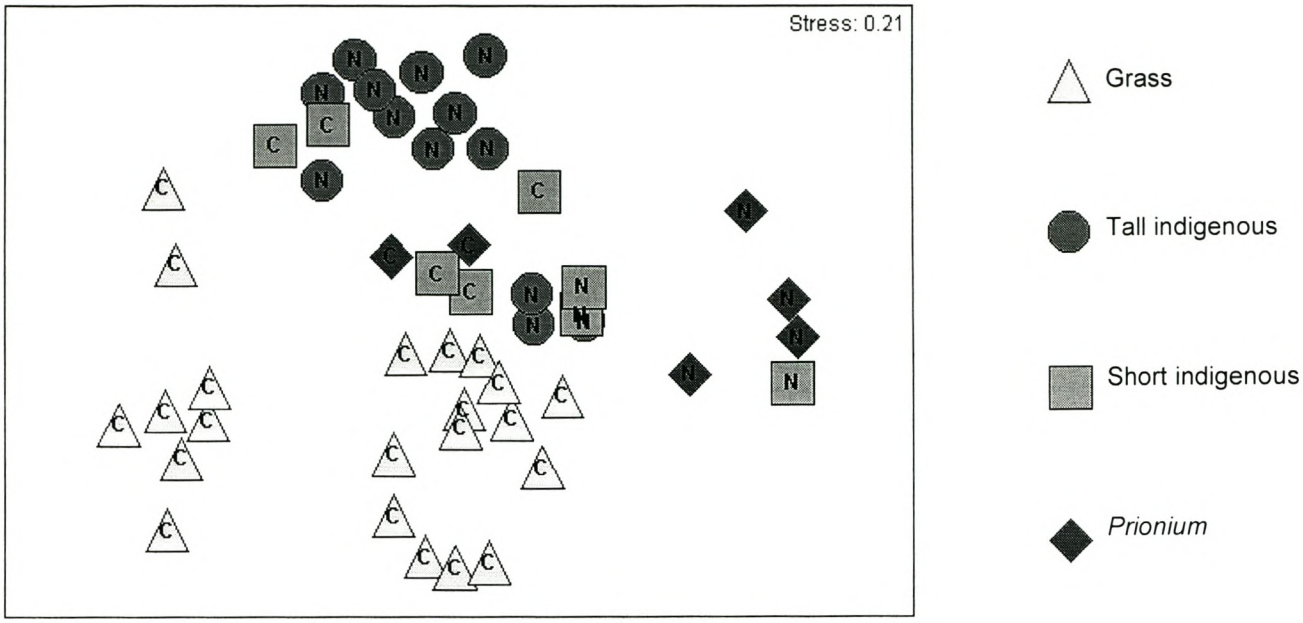


Fig. 6. MDS plot of Odonata species abundance data in cleared (C) and natural (N) sites, showing grouping according to dominant vegetation type.

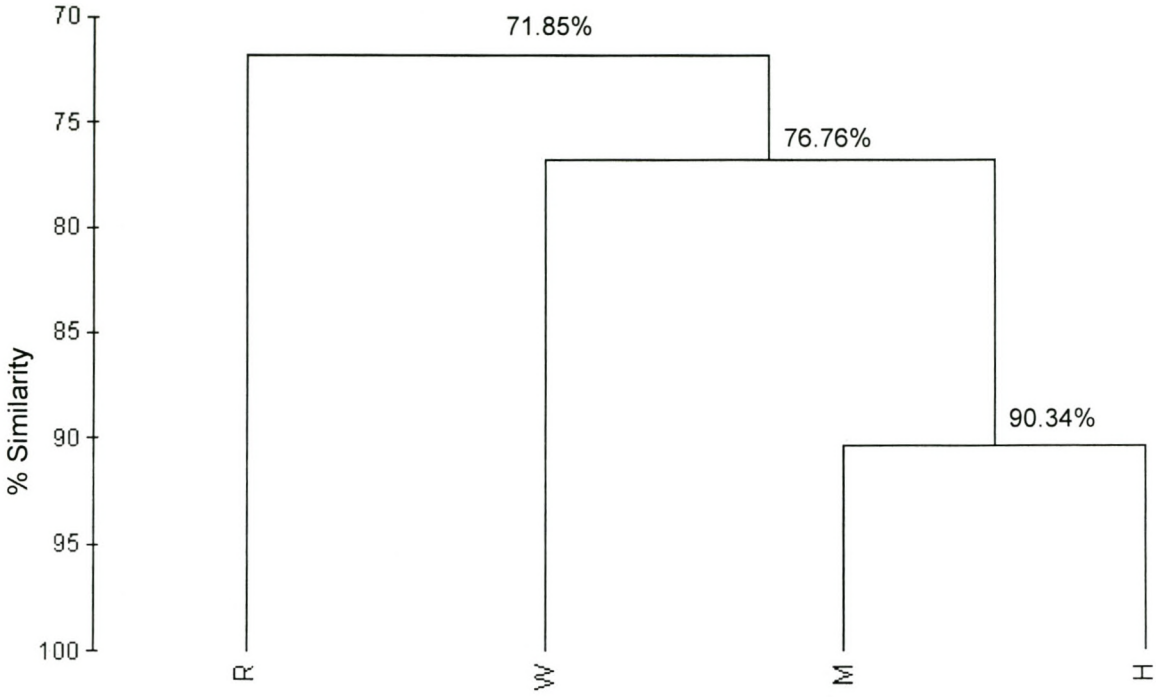


Fig. 7. Dendrogram of Rondegat (R), Witte (W), Molenaars (M) and Holsloot (H) rivers, based on hierarchical clustering of averaged fourth-root transformed species abundance data.

Table 3

Comparison of mean abundance and species richness between rivers and months. Subscripts indicate significantly higher values ($P < 0.05$).

	Mean abundance (± SE)	**Mean species richness** (± SE)
River		
Molenaars	6.66 ± 0.84	3.47 ± 0.31
Holsloot	6.03 ± 0.56	3.88 ± 0.24
Wit	8.62 ± 0.72	3.85 ± 0.31
Rondegat	6.02 ± 0.61	4.02 ± 0.35
ANOVA (rivers)	$F_{3, 244} = 3.10$, $P < 0.05$	$F_{3, 244} = 1.77$, $P = 0.16$
Month		
December	$6.65 \pm 0.97_{(Apr, May)}$	$8.29 \pm 0.95_{(Apr, May)}$
January	$7.59 \pm 1.16_{(Mar, Apr, May)}$	$9.53 \pm 1.00_{(Mar, Apr, May)}$
February	$6.53 \pm 1.03_{(Apr, May)}$	$8.53 \pm 0.95_{(Apr, May)}$
March	$5.00 \pm 0.70_{(Apr, May)}$	$6.18 \pm 0.83_{(Apr, May)}$
April	$2.90 \pm 0.39_{(May)}$	$2.71 \pm 0.34_{(May)}$
May	0.90 ± 0.21	1.65 ± 0.21
ANOVA (months)	Dec - May $F_{5,96} = 9.67$, $P < 0.001$	Dec - May $F_{5,96} = 17.64$, $P < 0.001$
	Dec - Mar $F_{3,64} = 1.20$, $P = 0.3$	Dec - Mar $F_{3,64} = 2.27$, $P = 0.09$

grass sites, irrespective of disturbance regime. Moreover, species assemblages in short indigenous bushes were more similar to tall indigenous trees than to *Prionium*.

With the exception of the Molenaars and Witte alien sites, there was a more pronounced grouping according to disturbance regime (Fig. 5A) than according to river (Fig. 5B). The Witte and Molenaars alien sites were very dense and were the least similar to the other sites. Fig. 7 gives the CLUSTER dendrogram of rivers, based on averaged species abundance data. The lowest similarity level was 72% for all four rivers. This was considerably greater than the percentage similarity between alien, cleared and natural sites (only 56% similarity, Fig. 3), indicating that pooled river data did not completely override the effects of alien vegetation and its removal.

ANOSIM2 yielded no significant difference between rivers (R = 0.012, P = 0.3). However, ANOSIM (with replicates) yielded a significant difference between Holsloot, Witte and Rondegat Rivers at $P \leq 0.001$ ($R > 0.426$), but not between the Molenaars and Holsloot Rivers ($R = 0.143$), the Molenaars and Witte Rivers ($R = 0.187$) and the Molenaars and Rondegat Rivers ($R = 0.212$). There was, however, no significant difference between rivers at $P = 0.01$. ANOVA of univariate abundance data also found no significant difference between rivers at $P = 0.03$, but the difference was significant at $P = 0.01$ (Table 3). ANOVA of species richness data revealed no significant difference between rivers at $P = 0.16$. Student's t-tests also revealed no significant difference between rivers at $P < 0.05$.

3.3. Species responsible for assemblage patterns

Having established that species abundance patterns reflected disturbance regime, SIMPER was then used to establish which species of Odonata explained these patterns (Table 4). Natural sites with indigenous trees as the dominant vegetation type were characterised predominantly by *T. furva/dorsalis*, *Allocnemis leucosticta*, *Elattoneura frenulata* and *Aeshna subpupillata*. Near-

natural sites, with and abundance of *Prionium* and recovering fynbos, were characterised by *Pseudagrion furcigerum*, *E. frenulata* and *Anax speratus*. Overall, cleared areas were characterised by *T. furva/dorsalis*, *P. furcigerum*, *Anax speratus*, *Orthetrum julia capicola* and *E. frenulata* (Table 4).

SIMPER analysis of only cleared sites found *E. frenulata* and *P. furcigerum* to be characteristic of sites with dominant *Prionium* growth (each species contributing 43 and 30% of the total abundance respectively) (Table 4). *T. furva/dorsalis*, *A. speratus* and *O. julia capicola* were strongly associated with dominant grass growth (39% contribution). *T. furva/dorsalis*, *P. furcigerum* and *E. frenulata* were associated with dominant short indigenous bushes (48% contribution). (*Prionium* was often also abundant in the latter sites).

Dense alien sites were characterised by only two species, *C. umbratus* and *O. julia capicola*. Alien sites with lower tree densities had a high abundance of species generally associated with cleared sites, including *T. furva/dorsalis*, *P. furcigerum* and *A. speratus*.

Assemblages differed between rivers, as well as between sites (Table 5). The Holsloot and Rondegat alien sites were more open and exposed and had species assemblages similar to cleared sites, with a relatively high abundance of *T. furva/dorsalis* and *P. furcigerum*. The high abundance of *A. subpupillata* in cleared Holsloot sites is probably explained by the relatively good recovery of indigenous fynbos in these sites, while the abundance of *P. furcigerum* in natural Holsloot sites was probably a response to abundant *Prionium* growth in two of the sites. The Witte River was unusual in having *O. julia capicola* prominent in cleared areas, which were generally dominated by grass and *Prionium*. The natural sites along the Rondegat River had been burnt in the past year, resulting in a more open, grassy vegetation, thus explaining the abundance of *A. speratus* and *O. julia capicola*. The cleared areas were also dominated by grassy vegetation and *T. arteriosa* was prominent here.

The CCA ordination diagram of species and the environmental variables affecting their distribution (Fig. 8) visually represents these associations. This is purely a means of visualising environmental preferences by examining the distribution of species along environmental gradients. The CCA and SIMPER results are not directly comparable as they are based on different methodologies. (The latter is based on absolute abundances, independent of environmental influences; the former is based on relative abundances in response to environmental influences.) While SIMPER gives the species assemblages characteristic of particular habitats, CCA gives the weighted average position of each species along the individual environmental gradients. (The overall effects of environmental variables are discussed in greater detail in section 3.5). Fig. 8 is used purely to visually represent the responses of the most abundant species to biotope-specific gradients, remembering that physical factors, such as oxygen and width, may also have influenced the position of species on the ordination diagram. (However, when physical factors were removed from the CCA, the ordination diagram was largely unaltered, suggesting that physical factors had less influence on species distribution patterns.)

Fig. 8 shows that *A. leucosticta* was clearly associated with an abundance of tall indigenous trees and the lowest levels of alien cover. *E. frenulata* and *A. subpupillata* were associated with sunlit conditions with an abundance of, indigenous vegetation (both short and tall), exposed rocks and natural sites. Unlike SIMPER, the association of *E. frenulata* with *Prionium* is less evident. This is probably because *Prionium* was correlated with the third axis, which accounted for very little variation in species patterns (eigenvalue = 0.06). However, most of the variability of *E. frenulata* was accounted for by this axis, together with axis 4, this information having been lost in the conversion of the data to a two-dimensional ordination diagram. Nevertheless, in the ordination diagram, *E. frenulata* is closer to cleared and near-natural sites (with abundant *Prionium* and short fynbos growth) than *A. leucostica* and *A. subpupillata.*

C. *umbratus* was an outlier, associated with high levels of alien cover, shade (canopy cover) and exposed banks, all typical conditions in dense alien sites. *P. furcigerum* and *O. julia capicola* were associated with an abundance of *Prionium* and with near-natural sites. They were also apparently able to tolerate low levels of shade (canopy cover) and alien trees. *P. kersteni*, *T. arteriosa*, *C. sanguinolenta* and *A. speratus* were all associated with above average levels of grass, sedge and short indigenous vegetation and with cleared and less dense alien sites. *T. furva/dorsalis* was associated with warm, sunny conditions with relatively high availabilities of exposed rocks, grass and sedge and of both short and tall indigenous vegetation.

In both SIMPER and CCA, *A. leucosticta*, *A. subpupillata* and *E. frenulata* were closely associated with natural sites (Fig. 8, Table 4). In fact, of the natural sites (averaged over the four months), 67% had all three species present and 33% had two of the three species. There were no samples represented by only one of the three species and *A. leucosticta* was present in all natural sites (near-natural sites excluded). In cleared sites, there was greater complementarity. Only 10% of sites had all three species present, 19% had two species and where only one species occurred, this was never *A. leucosticta*. *E. frenulata* appeared to be more common than the other two species in cleared and near-natural sites (Table 4, Fig. 8), being present in all near-natural sites. The three species never occurred together in near-natural, alien or dense alien sites.

To establish the similarity between the abundance patterns of these three species across sites, a cluster analysis, based on Bray-Curtis similarities, was performed of species (excluding rare species), based on the sites they occurred in. The overall similarity between all 12 common species was 15.09%. There was only 37.74% similarity between *A. subpupillata*, *A. leucosticta* and *E. frenulata.* The greatest similarity between any two species was between *E. frenulata* and *T. furva/dorsalis* (59.3% similarity) and then between these two species and *A. speratus* (49.5% similarity). The next most similar species were *A. subpupillata* and *A. leucosticta* (46.38% similarity to each other). Considering only natural sites, *A. leucosticta* and *A. subpupillata* were

Table 4

Characteristic species of Odonata for each disturbance regime (and dominant vegetation type), based on SIMPER analyses. Only abundant species that cumulatively contributed up to 80% of the abundance are recorded. South African endemics are marked with an asterisk.

Natural (Tall indigenous trees)	**Near-natural (*Prionium*)**	**Cleared**	**Alien (medium density)**	**Dense alien (high density)**
Trithemis furva/dorsalis *Allocnemis leucosticta** *Elattoneura frenulata* *Aeshna subpupillata**	*Pseudagrion furcigerum** *Chlorolestes umbratus** *Elattoneura frenulata* *Anax speratus*	**(Grass)** *Trithemis furva/dorsalis* *Anax speratus* *Orthetrum julia capicola** *Pseudagrion furcigerum** **(Short indigenous bushes)** *Trithemis furva/dorsalis* *Pseudagrion furcigerum** *Elattoneura frenulata* *Orthetrum julia capicola** *Anax speratus* ***(Prionium)*** *Pseudagrion furcigerum** *Elattoneura frenulata* *Anax speratus* *Trithemis furva/dorsalis*	*Trithemis furva/dorsalis* *Pseudagrion furcigerum**	*Chlorolestes umbratus** *Orthetrum julia capicola**

Table 5

SIMPER analysis of Odonata species data, showing characteristic assemblages in cleared, natural and alien sites in all rivers (total), and for each of the Molenaars, Holsloot, Witte and Rondegat Rivers. Only species that cumulatively contributed over 80% of the total abundance are recorded. Species that were present in individual river assemblages but were absent from the total assemblages (from pooled data from all rivers), are in bold.

Total	Molenaars	Holsloot	Witte	Rondegat
Natural				
Trithemis furva/dorsalis	*Trithemis furva/dorsalis*	*Aeshna subpupillata*	***Pseudagrion furcigerum***	*Trithemis furva/dorsalis*
Allocnemis leucosticta	*Elattoneura frenulata*	*Trithemis furva/dorsalis*	***Chlorolestes umbratus***	*Elattoneura frenulata*
Elattoneura frenulata	*Aeshna subpupillata*	*Allocnemis leucosticta*	*Elattoneura frenulata*	***Anax speratus***
Aeshna subpupillata	*Allocnemis leucosticta*	***Pseudagrion furcigerum***		*Allocnemis leucosticta*
				Orthetrum julia capicola
Cleared				
Trithemis furva/dorsalis	*Trithemis furva/dorsalis*	*Trithemis furva/dorsalis*	*Orthetrum julia capicola*	*Trithemis furva/dorsalis*
Pseudagrion furcigerum	*Pseudagrion furcigerum*	*Pseudagrion furcigerum*	*Trithemis furva/dorsalis*	***Trithemis arteriosa***
Anax speratus	*Anax speratus*	***Aeshna subpupillata***	*Anax speratus*	*Elattoneura frenulata*
Orthetrum julia capicola	*Orthetrum julia capicola*	*Anax speratus*		*Anax speratus*
Elattoneura frenulata	*Elattoneura frenulata*			
Alien				
Trithemis furva/dorsalis	*Chlorolestes umbratus*	*Trithemis furva/dorsalis*	*Chlorolestes umbratus*	*Trithemis furva/dorsalis*
Orthetrum julia capicola		*Pseudagrion furcigerum*	*Orthetrum julia capicola*	
Chlorolestes umbratus				
Pseudagrion furcigerum				

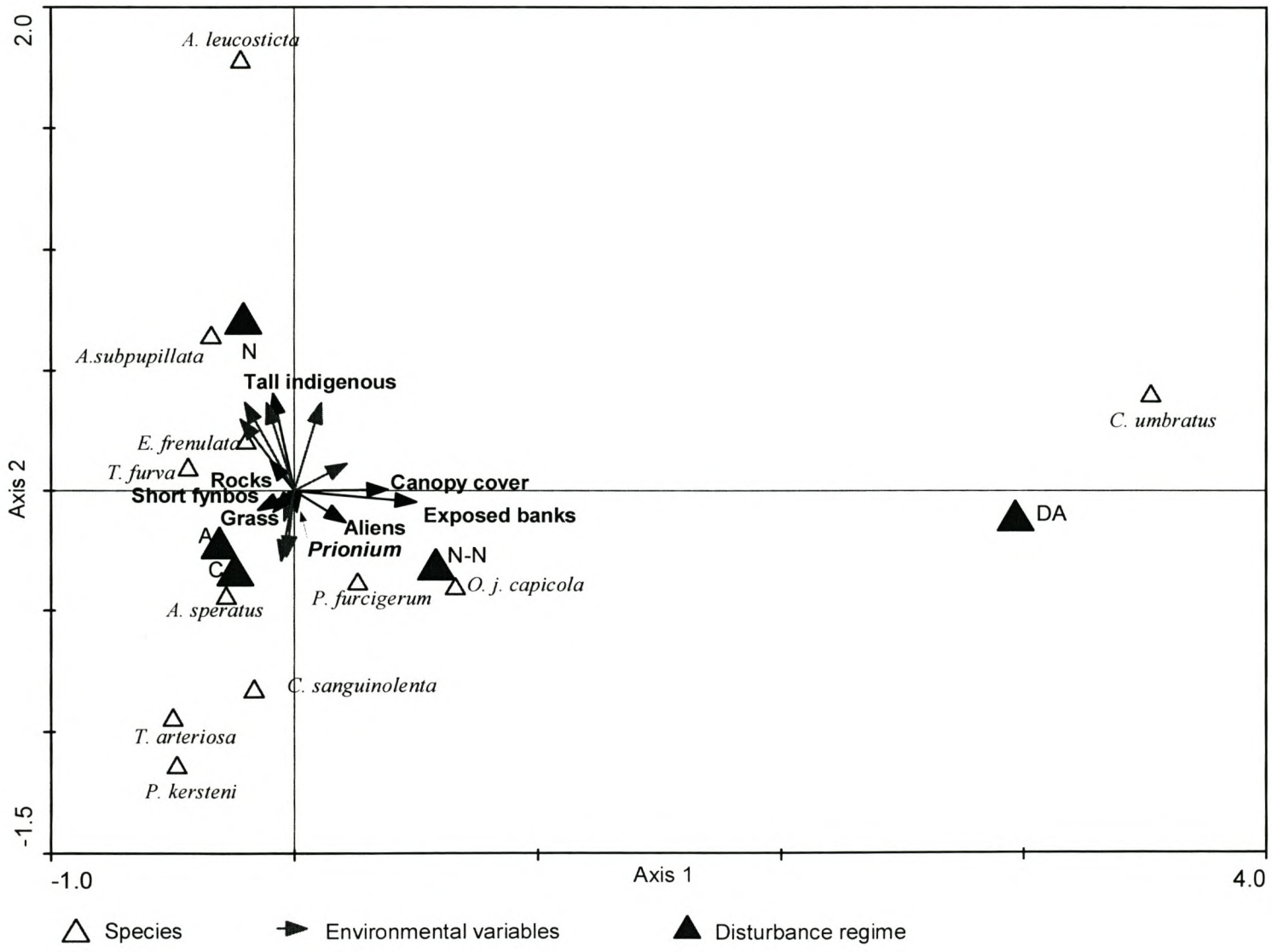


Fig. 8. Canonical Correspondance Ordination diagram of environmental variables and commonly occurring species (>2.5% of the total abundance) in the four rivers. Only vegetation- and biotope-specific variables are labelled. Disturbance regime site classes are represented by centroids. C = Cleared, N = Natural, N-N = near-natural, A = Alien, DA = Dense alien.

most similar to each other (71.6%), while in cleared sites, *A. subpupillata* and *E. frenulata* were most similar (57.9%).

According to the SIMPER results, the species responsible for distinguishing between natural and cleared sites included *A. leucosticta*, *P. furcigerum*, *A. subpupillata* and *E. frenulata* (7.24% dissimilarity). Distinguishing species for natural and alien sites included *A. leucosticta*, *E. frenulata*, *T. furva/dorsalis* and *A. subpupillata* (10.33% dissimilarity). Distinguishing species for cleared and alien sites were *T. furva/dorsalis*, *P. furcigerum*, *E. frenulata* and *O. julia capicola* (9.29% dissimilarity). These are all potential indicator species and were analysed further using the Indicator Value method.

3.4. Indicator species and monitoring

Table 6 gives the indicator values for the characteristic species in natural, near-natural, cleared and alien sites. The indicator value of *A. leucosticta* was high enough to be considered a potential indicator species for natural (tall indigenous) sites, while *P. furcigerum* could be considered a potential detector species for near-natural (*Prionium*) sites. The mean abundance of these species in each vegetation type (Fig. 9) shows that *P. furcigerum* is abundant in sites with dominant *Prionium* and short indigenous vegetation but is less abundant in sites with tall indigenous trees (which had less *Prionium* growth). Fig. 9 also shows that *A. subpupillata* and *E. frenulata* had a more even distribution across vegetation types. *E. frenulata*, A. *leucosticta* and *A. subpupillata* were all abundant in natural sites with tall indigenous trees, but *A. subpupillata* and *E. frenulata* had less specific vegetation preferences and were also abundant in natural or cleared sites with other vegetation types. *E. frenulata* was most abundant in *Prionium* sites, although less so than *P. furcigerum*.

Seasonal and regional differences affected indicator values (Table 7). However, the indicator values for *A. leucosticta* were consistent between rivers and between months, but not after

Table 6

Indicator values (in brackets) for characteristic species in alien, cleared and natural habitats. Indicator values were calculated from Odonata species abundance data collected monthly between December and February from the Molenaars, Holsloot, Witte and Rondegat Rivers. Potential indicator and detector species are in bold.

Natural	Near-natural	Cleared	Alien
***Allocnemis leucosticta* (72.74)**	***Pseudagrion furcigerum* (67.47)**	*Trithemis furva/dorsalis* (41.44)	*Chlorolestes umbratus* (9.46)
Trithemis furva/dorsalis (35.45)	***Zygonyx natalensis* (53.93)**	*Pseudagrion kersteni* (24.78)	*Trithemis furva/dorsalis* (4.87)
Aeshna subpupillata (25.12)	*Elattoneura frenulata* (41.78)	*Orthetrum julia capicola* (21.90)	*Orthetrum julia capicola* (3.76)
Elattoneura frenulata (20.34)	*Anax speratus* (29.57)	*Anax speratus* (18.05)	*Pseudagrion furcigerum* (1.18)
Paragomphus cognatus (11.95)	*Chlorolestes umbratus* (23.40)	*Aeshna subpupillata* (17.67)	
Anax speratus (10.46)		*Pseudagrion furcigerum* (12.63)	

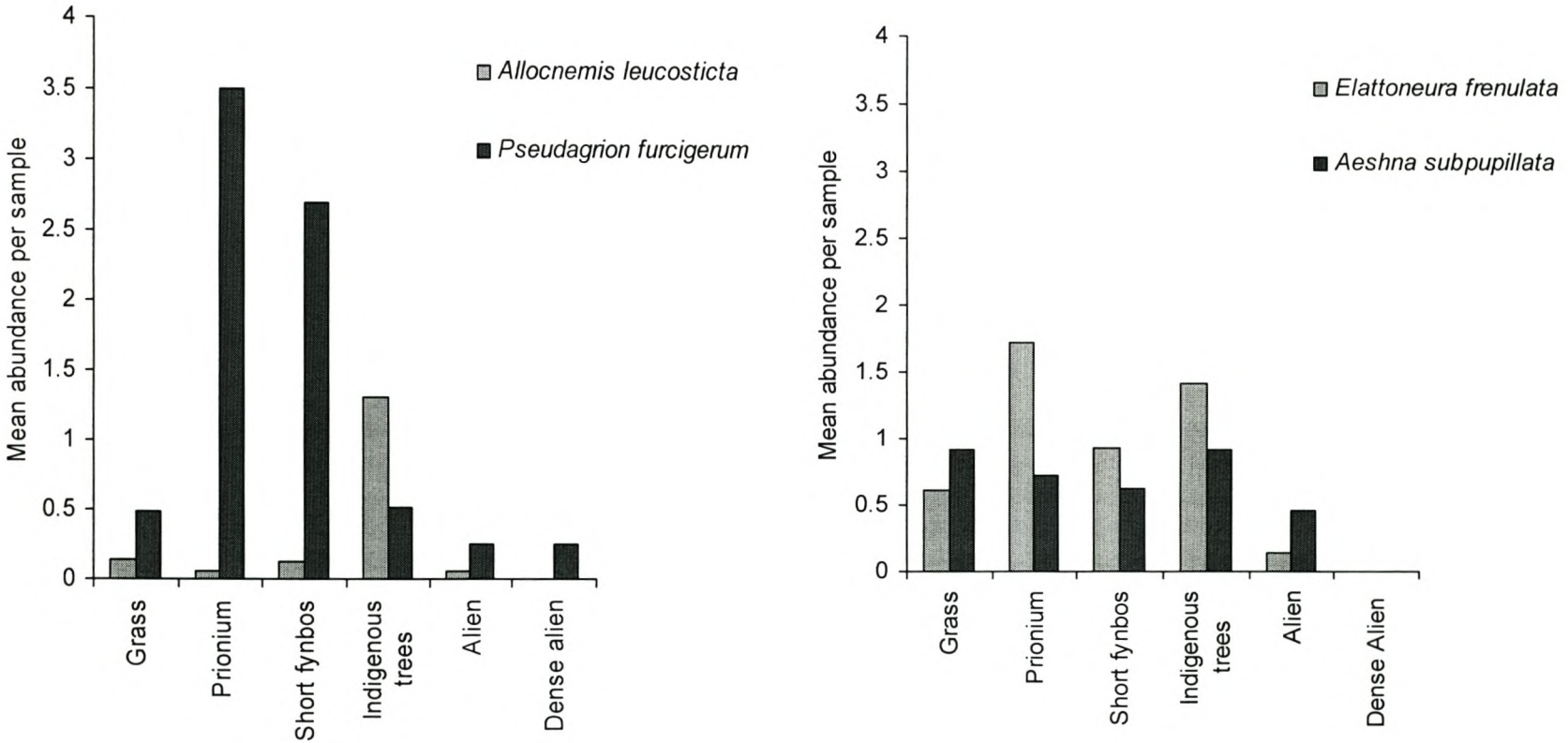


Fig. 9. Mean abundance per sample of *Allocnemis leucosticta*, *Pseudagrion furcigerum*, *Elattoneura frenulata* and *Aeshna subpupillata* in each dominant vegetation type.

Table 7

Indicator values for potential indicator and detector species (in bold) in natural, cleared and alien habitats, showing variation between rivers and between months.

	Molenaar	Holsloot	Witte	Rondegat	Dec	Jan	Feb	Mar	Apr
Natural (Tall indigenous)									
Allocnemis leucosticta	**70.59**	**93.33**		**80**	**72.14**	**75.46**	**70**	5	0
Elattoneura frenulata	**62.01**	8.28		**51.63**	15.43	16.07	24.66	10.9	0
Pseudagrion furcigerum	0.23	27.27		**73.33**	3.86	6.23	0	0.38	11.67
Near-natural (*Prionium*/short indigenous)									
Pseudagrion furcigerum			**76.03**		**86.59**	**71.06**	**58.56**	0	0
Elattoneura frenulata			**74.53**		48.6	**55.79**	24.66	0	0
Chlorolestes umbratus			33.33		13.55	2.8	25.71	**71.02**	**70.79**
Zygonyx natalensis			**66.67**		**61.74**	**85.14**	31.11	0	0
Cleared (grass/short indigenous)									
Trithemis furva/dorsalis	47.69	33.49	**76.67**	**63.38**	40.32	39.68	40.36	**65.42**	30.95
Pseudagrion furcigerum	**69.72**	**61.51**	20.77	0	22.87	26.76	36.54	21.4	2.32
Orthetrum julia capicola	32.35	26.67	**85.96**	6.27	28.53	7.87	38.38	48.7	4.76
Pseudagrion kersteni	44.44	8.57	26.66	21.33	4.76	44.9	28.99	43.51	**57.2**

February. Similarly, *P. furcigerum* could only be regarded as a detector species between December and February, and only in near-natural sites. The high indicator values for *Zygonyx natalensis* were undoubtedly a response to flow regime and not to vegetation type.

All other species had inconsistent indicator values across rivers and months. Only the Witte River cleared sites had high indicator values for *T. furva/dorsalis* and *O. julia capicola*. *Elattoneura frenulata* had an indicator value sufficiently high to be regarded as a detector species in natural sites along the Molenaars and Rondegat Rivers. Indicator values were high for *T. furva/dorsalis* in March and for *Pseudagrion kersteni* in April. In the Witte River near-natural sites, *C. umbratus* had high indicator values in March and April.

3.5. Environmental effects on assemblage patterns

The BIO-ENV procedure revealed that the environmental variable that best reflected assemblage patterns was percentage canopy cover ($P = 0.47$). The best overall combination of variables was percentage canopy cover, short indigenous vegetation, percentage exposed rocks, pH and conductivity ($P = 0.65$). Of these, the highest correlations were with variables that indicated biotope availability (vegetation type, shading, exposed rocks) (i.e. $P = 0.47$ for canopy cover; $P = 0.55$ for short indigenous vegetation and $P = 0.33$ for percentage exposed rocks), rather than variables relating to physical conditions ($P = 0.28$ for pH and $P = 0.16$ for conductivity).

Different environmental variables appeared to be important in different rivers (Table 8). However, in all rivers, vegetation appeared to be of dominant importance, either directly or indirectly – i.e. canopy cover, short/tall indigenous vegetation, *Prionium*, grass and exposed banks. All these factors are affected by the degree of alien invasion or alien removal. Conductivity and pH did not show strong correlations for within-river analyses, indicating that they primarily reflected differences between rivers.

CCA confirmed the overall importance of canopy cover and pH, but found the effects of exposed rocks and short indigenous vegetation to be statistically insignificant (Table 9). Conductivity was less important, but still significant. This discrepency between the CCA and BIO-ENV results stems from differences in the two methodologies. CCA is based on chi-square distance measures that compares relative abundances, while BIO-ENV is based on euclidean distance measures of absolute abundances. For this reason, CCA tends to emphasise the infrequent, rarer and more specialised species and differences in total abundance among sites do not necessarily increase the dissimilarity (ter Braak and Verdonschot, 1995).

It is also possible that unmeasured environmental variables were unaccounted for in the CCA, which is constrained by the supplied environmental variables. Therefore, a Correspondence Analysis (CA), which is an indirect gradient analysis and, hence, not constrained, was performed. A comparison of the CCA and CA eigenvalues indicated only minor differences between the first two axes (Table 10). In addition, the same set of environmental variables correlated with at least the first two axes of each ordination. This indicates that, while there were outstanding environmental variables, the environmental variables supplied accounted for most of the species composition patterns. The Monte Carlo test confirmed that the measured environmental variables accounted for a significant amount of the variation of the first axis (F = 11.296, P = 0.002) and the overall ordination (F = 3.799, P = 0.002). The species-environment correlation was strong (greater than 0.87 on all axes) and the environmental variables were responsible for the main variation in species patterns (cumulative percentage variance of species data and species-environment relations = 77.6%) (Table 10). The total inertia was 1.13.

Fig 10 gives the CCA ordination diagram of environmental variables, with disturbance classes represented as centroids. Figs 11 and 12 give the ordination diagram of environmental variables and sites, the latter grouped according to status (Fig. 11) and river (Fig. 12). The arrow lengths demonstrated the importance of bank exposure, dissolved oxygen, pH, tall indigenous trees and

canopy cover. Bank exposure and canopy cover both showed the strongest correlation with axis 1 (Table 9). Axis 1 was more important than axis 2 in explaining the observed species distributions (eigenvalues 0.28 and 0.21 respectively). Percentage tall indigenous trees, width and depth were strongly correlated with the second axis. Shade and canopy cover were strongly co-correlated (r = 0.89), as were conductivity and percentage *Eucalyptus* cover (r = 0.82). Shade and canopy cover were therefore treated as a single variable in the ordination, as were percentage *Eucalyptus* and conductivity. For visual clarity, variables unrelated to alien disturbance and found to be unimportant by both CCA and BIO-ENV (percentage riffle, gravel, sand, pool and cobbles) were also excluded from the ordination.

Species distribution patterns were clearly grouped according to disturbance regime (Fig. 11). Alien sites showed great variability in terms of bank exposure, canopy cover and shade (axis 1), as well as in terms of conductivity, suspended solids, depth and flow (axis 2). When considered as a nominal variable, the dense alien site class was correlated primarily with axis 1 and the less dense alien site class with axis 2 (Fig. 10). Species assemblages in dense alien sites (> 70% alien cover) were associated with above average canopy cover, exposed banks and flow rate. Less dense alien sites had very similar species assemblages and species-environment relations to cleared sites. These sites were distributed along a gradient of temperature, suspended solids, conductivity (and *Eucalyptus* cover) and depth (Fig. 11). On average (Fig. 10), species assemblages in these sites were associated with an abundance of short indigenous vegetation and grass, as well as sunlit conditions with high temperatures, suspended solids and conductivity.

In general, species assemblages in natural sites were associated with higher oxygen levels, pH and tall indigenous tree cover (Figs 10 and 11). Conversely, mean temperature, conductivity, suspended solids, bank exposure and percentage cover of grass, *Prionium* and short indigenous vegetation were all below average in natural sites. In near-natural sites, species patterns were associated with high levels of *Prionium* growth and flow rates. The ordination plot also gives the

impression that these sites were associated with high levels of alien *Acacia* growth, bank exposure and canopy cover. However, the near-natural site class, when considered as a nominal variable, was most strongly correlated with axis 4 (Fig. 10), whereas alien growth, bank exposure and canopy cover were correlated with the first axis. This information is lost during the conversion of the multidimensional data to a two-dimensional plot. The fourth axis accounted for very little of the variation in species patterns (with an eigen value of 0.07).

Overall, the most important environmental variables affecting species distribution patterns (in descending order of importance) were: exposed banks, disturbance regime, dissolved oxygen, pH, tall indigenous vegetation, canopy cover (and therefore shade), width, depth, suspended solids, conductivity and river system (Table 9). All were statistically significant at $P < 0.01$. However, Fig. 12 shows strong grouping of sites according to rivers, indicating substantial differences between them. For instance, dense alien sites were located along the Witte and Molenaars rivers only, while tall indigenous trees were associated mostly with Molenaars and Holsloot natural sites, being completely absent from Witte River sites. This, together with the statistical significance of 'river system' as a nominal variable in the Monte Carlo test, indicated that between-river effects might have had a considerable influence on the results.

To factor out these effects, a partial CCA was performed with 'river' as a covariable (Table 11). With geographical effects thus removed, the most important variables (in descending order of importance) were percentage bank exposure, canopy cover, suspended solids and disturbance regime. Dissolved oxygen, pH, tall indigenous vegetation, width and conductivity decreased in importance, suggesting that these variables largely explained geographical differences in species abundance patterns, rather than alien disturbance effects. This is consistent with the BIO-ENV result. Canopy cover, suspended solids, flow rate and percentage cover of grass and *Prionium* increased in importance at the within-river level. Exposed rocks also had a significant effect at this level, but short indigenous vegetation did not.

Table 8

Environmental variables that collectively yielded the strongest correlation with Odonata assemblage patterns in each of the Molenaars, Holsloot, Witte and Rondegat Rivers, and overall (i.e. pooled data from all rivers). Factors that are directly affected by alien infestation and alien clearing are italicised.

Total (all rivers)	**Molenaars river**	**Holsloot River**	**Witte River**	**Rondegat River**
***r* = 0.671**	***r* = 0.921**	***r* = 0.711**	***r* = 0.829**	***r* = 0.791**
Canopy cover (%)	*Canopy cover* (%)	*Tall indigenous trees* (%)	*Canopy cover* (%)	*Canopy cover* (%)
Short indigenous bushes (%)	*Short indigenous bushes* (%)	Exposed rocks (%)	*Shade* (%)	*Short indigenous bushes* (%)
PH	Exposed rocks (%)	*Shade* (%)	*Grass/sedge* (%)	*Alien cover* (%)
Conductivity	Cobbles (%)	Width	*Prionium* (%)	*Grass/sedge* (%)
Exposed rocks (%)		Gravel (%)		*Exposed banks* (%)

Table 9

Canonical correlation coefficients between environmental variables and the first two axes of the CCA of Odonata species sampled from all four rivers. Environmental variables are arranged in descending order of importance (according to the fit of each variable, taken singly, indicated by its eigenvalue). *P* = significance level of the effect, as obtained from the Monte Carlo Permutation test. Canopy cover and shade were highly co-correlated and therefore considered as a single variable.

Variables	Eigenvalues	Canonical coefficients		*P*
		Axis 1	Axis 2	
% exposed banks	0.15	0.625	- 0.014	0.002
Disturbance regime	0.12	0.435	- 0.456	0.002
Dissolved oxygen	0.11	- 0.289	0.511	0.002
PH	0.10	- 0.317	0.420	0.002
% tall indigenous trees	0.09	- 0.135	0.573	0.002
% canopy cover (/shade)	0.09	0.480	0.051	0.002
Width	0.09	- 0.170	0.505	0.002
Depth	0.09	0.119	0.531	0.002
Total suspended solids (TSS)	0.08	- 0.048	- 0.427	0.002
Conductivity	0.08	- 0.042	- 0.386	0.004
River system	0.07	- 0.004	- 0.385	0.002
% *Eucalyptus* cover	0.06	- 0.187	- 0.251	0.008
Flow	0.05	0.273	0.177	0.012
% grass and sedge	0.05	- 0.103	- 0.144	0.016
% alien cover (*Acacia*)	0.05	0.265	- 0.160	0.014
% cobbles	0.05	- 0.002	0.325	0.018
% *Prionium*	0.05	0.035	- 0.122	0.018
Water temperature	0.04	- 0.054	- 0.171	0.034
% pool	0.04	- 0.067	- 0.321	0.030
% gravel and sand	0.04	- 0.294	- 0.050	> 0.05
% exposed rocks	0.04	- 0.134	0.177	> 0.05
% short indigenous fynbos	0.03	- 0.185	- 0.122	> 0.05
% riffle	0.03	0.247	- 0.040	> 0.05

Table 10

Summary of the CCA and CA outputs for the analysis of the four rivers.

Axes	CCA				CA			
	1	2	3	4	1	2	3	4
Eigenvalues	0.256	0.197	0.09	0.073	0.344	0.224	0.116	0.1
Species-environment correlations	0.871	0.94	0.931	0.882	0.855	0.935	0.722	0.887
Cumulative percentage variance:								
of species data	22.7	40.1	48	54.5	30.5	50.3	60.5	69.4
of species-environment relation	32.3	57.1	68.5	77.6	31.7	56.3	64	73.9

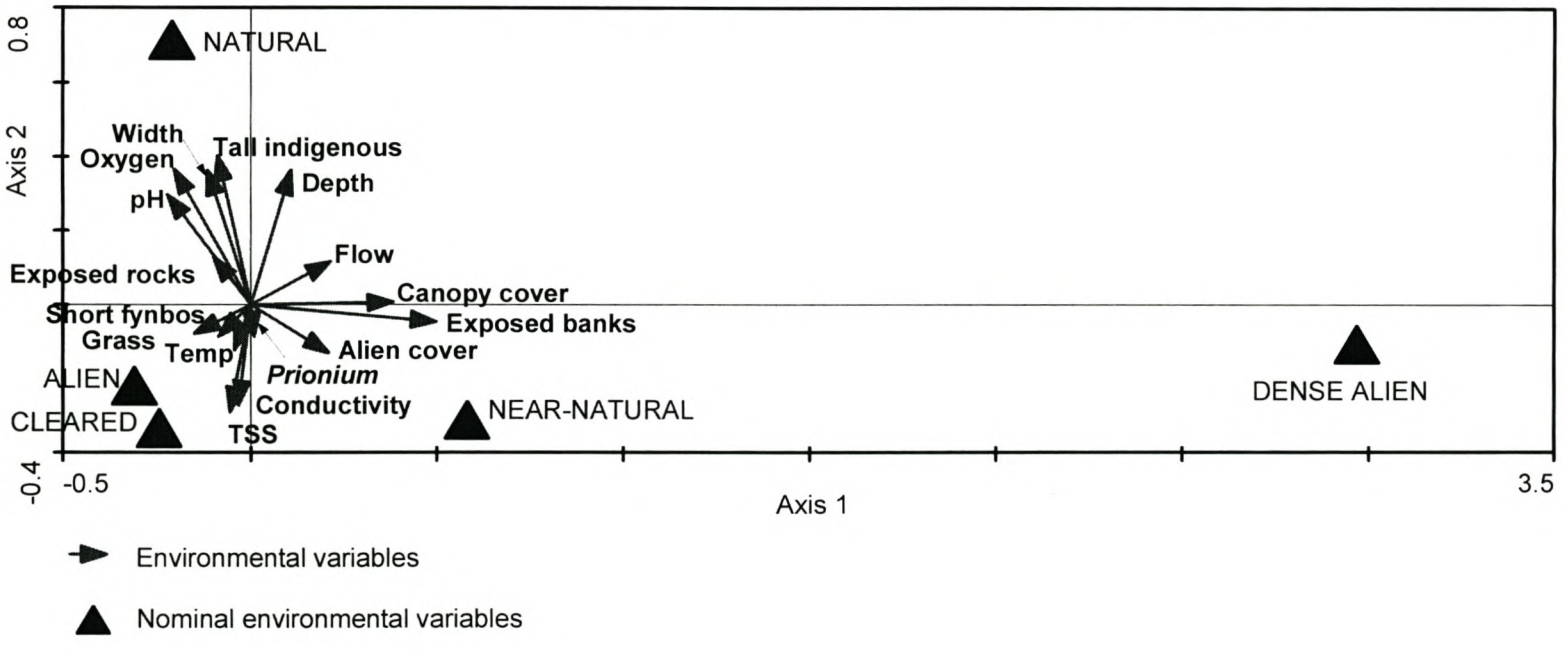


Fig. 10. Canonical Correspondence Analysis (CCA) ordination diagram of environmental variables affecting species distribution patterns in the four rivers. Disturbance regime classes are represented as centroids on the diagram. Axes lengths are in standard deviation units. Eigen values were 0.28 and 0.21 on axes 1 and 2 respectively. The variance accounted for by the first two axes was 56.2%. The full list of environmental variables is given in Table 2.

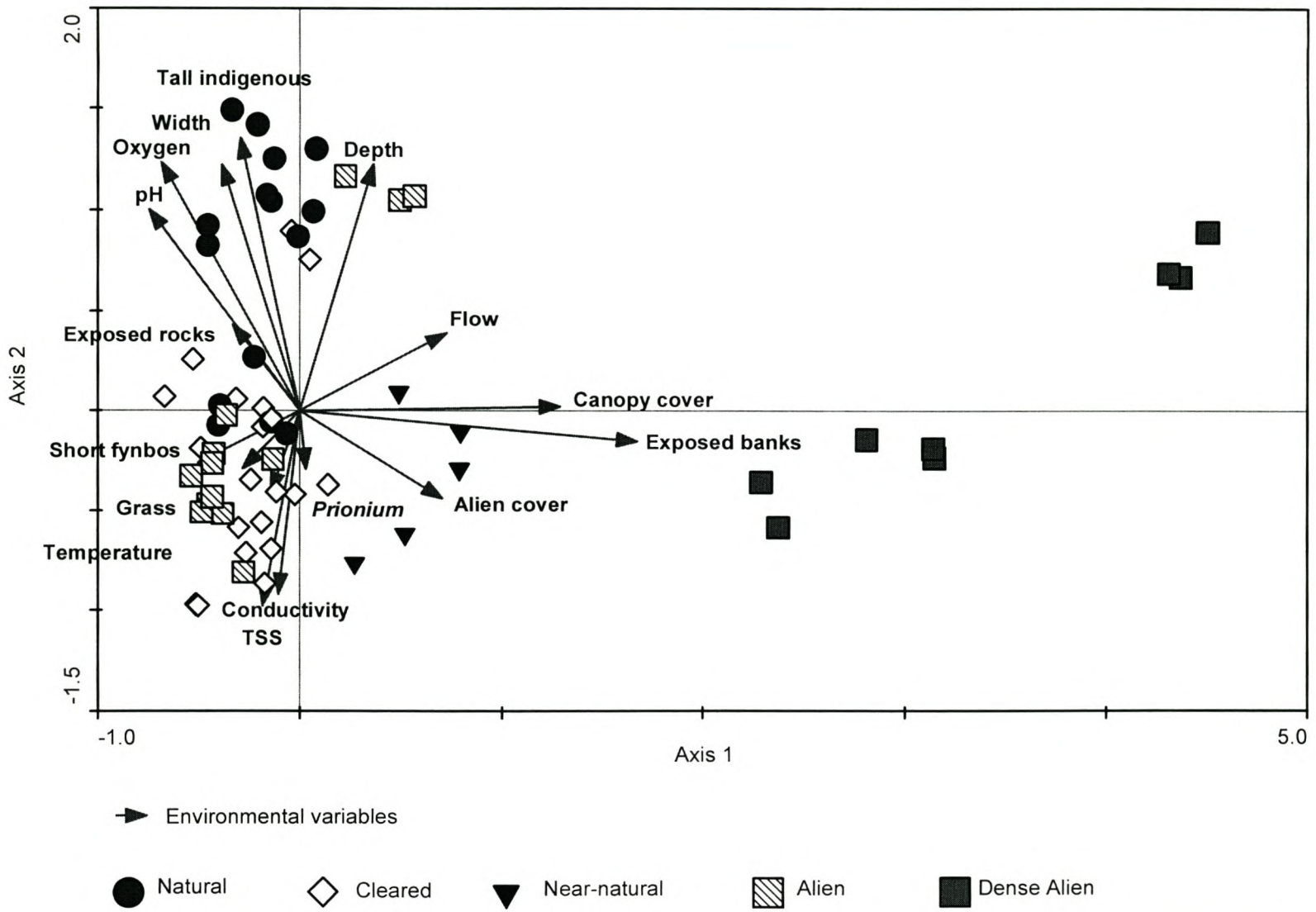


Fig. 11. CCA ordination diagram of sites and environmental variables affecting species distribution patterns across disturbance regimes in the four rivers. Eigen values are given in Table 1. The variance accounted for by the first two axes was 57%. Nominal variables and less important variables were excluded from the ordination. The full list of canonical correlation coefficients is given in Table 2.

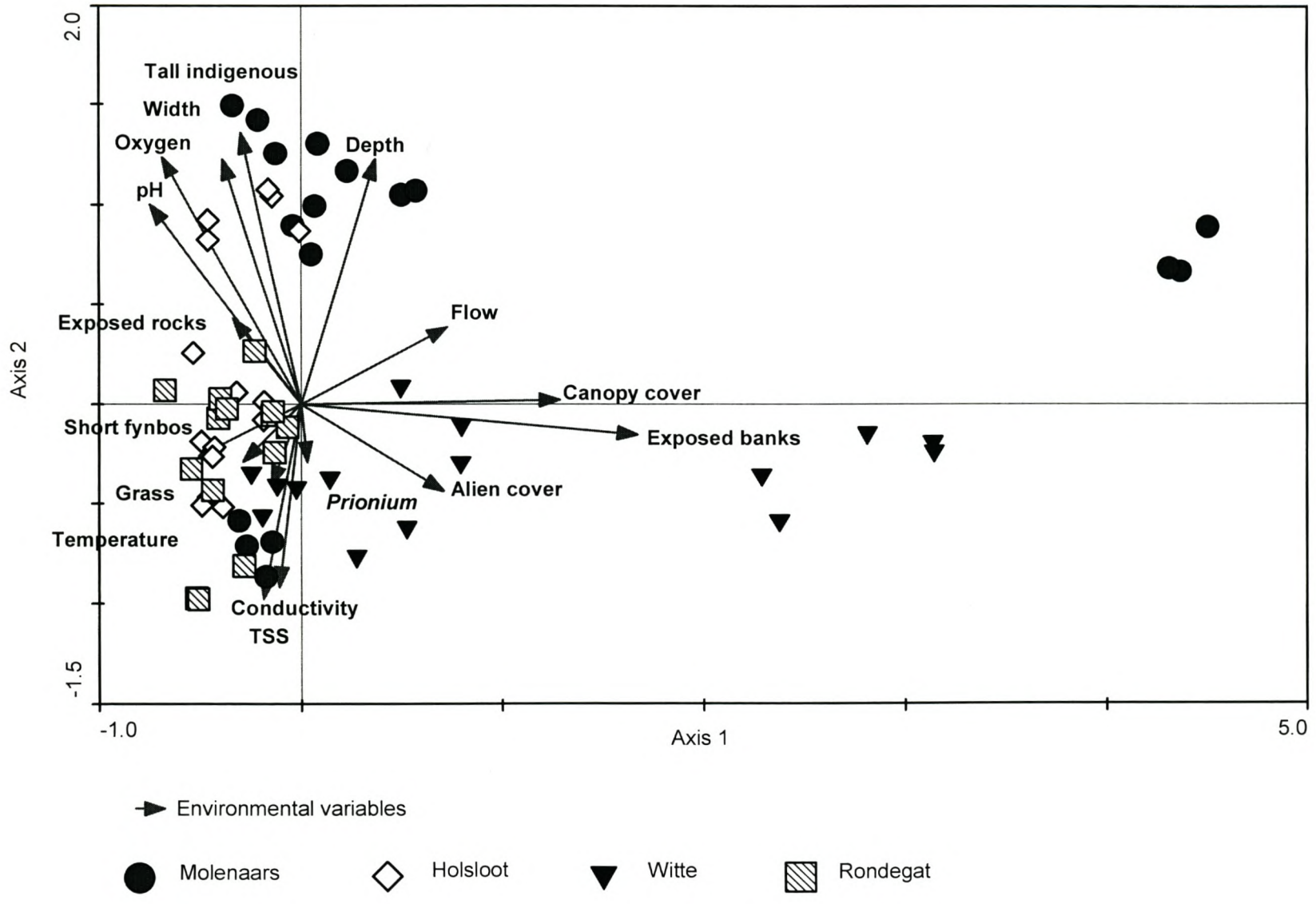


Fig. 12. CCA of sites and environmental variables affecting species distribution patterns across rivers. See Fig 1 for the disturbance regime of the sites.

Table 11

Canonical correlation coefficients between environmental variables and the first two axes of the CCA of Odonata species. The geographical effects across rivers were partialled out by taking the 'river system' class variable as a covariable. Environmental variables are arranged in descending order of importance (according to the fit indicated by the eigenvalues). *P* = significance level of the effect, as obtained from the Monte Carlo Permutation test. Canopy cover and shade were highly co-correlated and therefore considered as a single variable.

Variables	Eigenvalues	Canonical coefficients		P
		Axis 1	Axis 2	
% Exposed bank	0.13	0.634	- 0.074	0.002
% canopy cover (/shade)	0.11	0.485	0.018	0.002
Total suspended solids (TSS)	0.09	- 0.049	- 0.631	0.002
Disturbance regime	0.07	0.441	- 0.455	0.002
Depth	0.07	0.124	0.451	0.004
Flow	0.07	0.284	0.277	0.002
% grass and sedge	0.06	- 0.105	- 0.080	0.006
Width	0.06	- 0.210	0.342	0.012
% alien cover (*Acacia*)	0.05	0.266	- 0.201	0.004
% pool	0.05	- 0.069	- 0.417	0.006
% *Prionium*	0.05	0.038	- 0.330	0.018
PH	0.05	- 0.342	0.386	0.032
% cobbles	0.05	- 0.002	0.372	0.020
Conductivity	0.04	- 0.046	- 0.194	0.002
Dissolved oxygen	0.04	- 0.346	0.351	0.008
% riffle	0.04	0.120	0.308	0.002
% exposed rocks	0.04	- 0.138	0.321	0.040
% tall indigenous trees	0.04	- 0.181	0.451	0.018
% *Eucalyptus* cover	0.04	- 0.206	- 0.060	0.010
Water temperature	0.02	- 0.054	- 0.077	> 0.05
% short indigenous fynbos	0.02	- 0.192	- 0.002	> 0.05
% gravel and sand	0.01	- 0.296	- 0.005	> 0.05

With 'river system' partialled out, the Monte Carlo test again confirmed that the measured environmental variables accounted for a significant amount of the variation of the first axis (F = 11.49, P = 0.004) and the overall ordination (F = 3.36, P = 0.002). The species-environment correlation was strong (greater than 0.72 on all axes) and the environmental variables were responsible for the main variation in species patterns (cumulative percentage variance of species data and species-environment relations = 79.3%). The total inertia was 1.13.

3.5. Seasonal effects

Fig. 13 shows seasonal changes in the abundance of species. *C. umbratus* was clearly an autumn species, peaking in abundance in April, while *P. furcigerum*, *E. frenulata* and *A. leucosticta* were summer species, declining from February onwards. *E. frenulata* had a clear peak in January and February. With the exception of *T. arteriosa* and *O. julia capicola*, all Anisoptera declined in abundance from December onwards. *T. arteriosa* peaked in January and February and *O. julia capicola* peaked in February. This seasonal variability is likely to have affected species assemblage patterns. The species characteristic of each month, based on SIMPER analyses, are given in Table 12.

The CLUSTER analysis of averaged monthly data (Fig. 14) yielded a 77.1% similarity between December, January, February and March, while only 37.8% similarity existed between these months and April/May. This indicates that seasonal effects did not override the effects of disturbance regime during the analysis of pooled data from December to March. January and February were the most similar in terms of assemblage patterns (92.3%), followed by December to February (82.3% similarity).

ANOSIM showed that all months between December and February were significantly different to both April and May ($R > 0.926$, $P > 0.1$), but were not significantly different to each other at P =

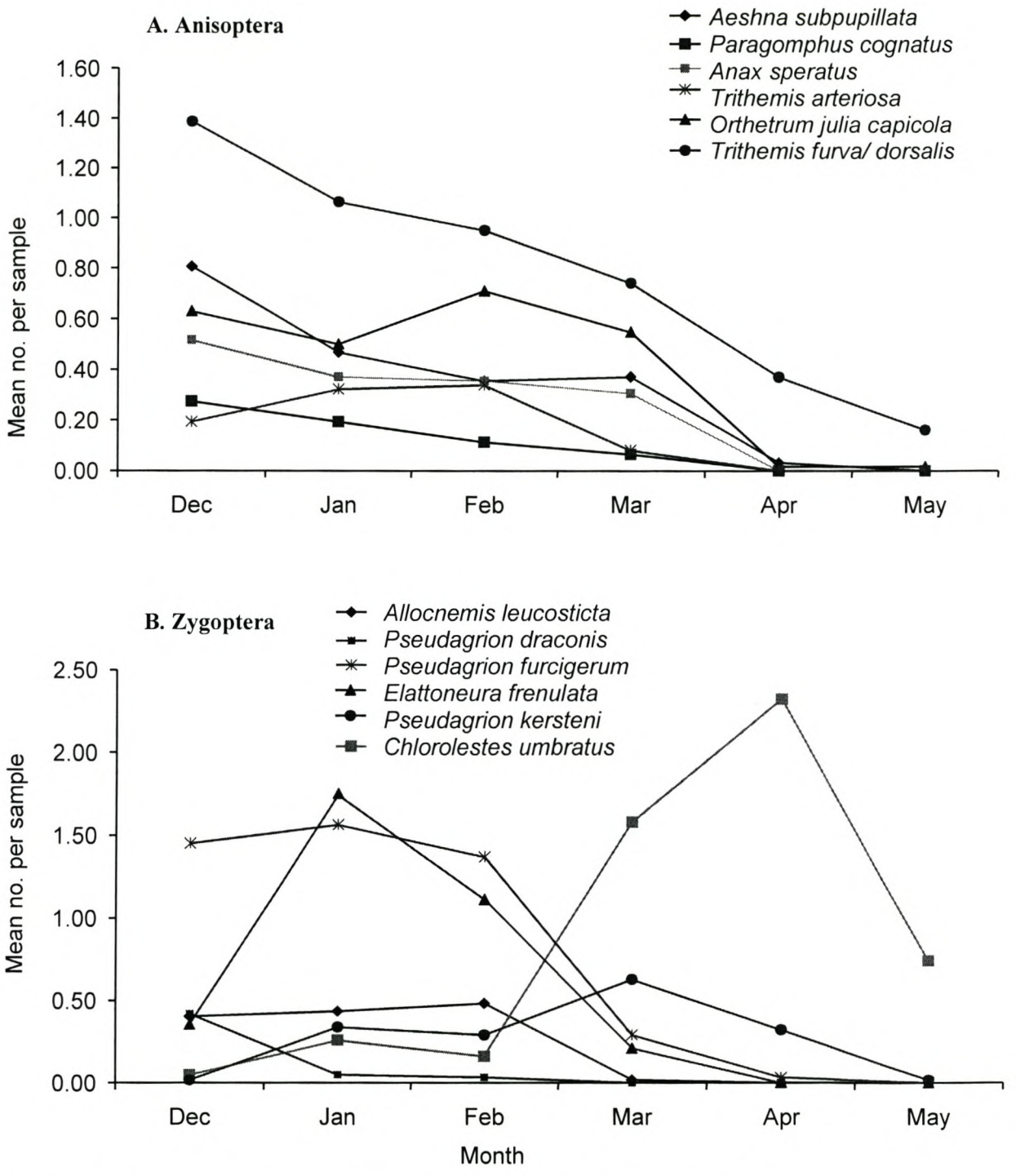


Fig. 13. Seasonal abundance of Odonata between December 2003 and May 2004. A. Anisoptera, B. Zygoptera

Table 12

Characteristic species of Odonata for each month, based on SIMPER analysis. Only abundant species that cumulatively contributed up to 80% of the abundance are recorded.

December	**January**	**February**
Trithemis furva/dorsalis	*Trithemis furva/dorsalis*	*Trithemis furva/dorsalis*
Pseudagrion furcigerum	*Elattoneura frenulata*	*Pseudagrion furcigerum*
Anax speratus	*Orthetrum julia capicola*	*Elattoneura frenulata*
Aeshna subpupillata	*Anax speratus*	*Orthetrum julia capicola*
Orthetrum julia capicola	*Aeshna subpupillata*	*Anax speratus*
Elattoneura frenulata	*Allocnemis leucosticta*	*Allocnemis leucosticta*
Pseudagrion draconis	*Pseudagrion kersteni*	*Chlorolestes umbratus*

March	**April**	**May**
Chlorolestes umbratus	*Chlorolestes umbratus*	*Chlorolestes umbratus*
Trithemis furva/dorsalis	*Trithemis furva/dorsalis*	*Trithemis furva/dorsalis*
Aeshna subpupillata		
Anax speratus		
Orthetrum julia capicola		

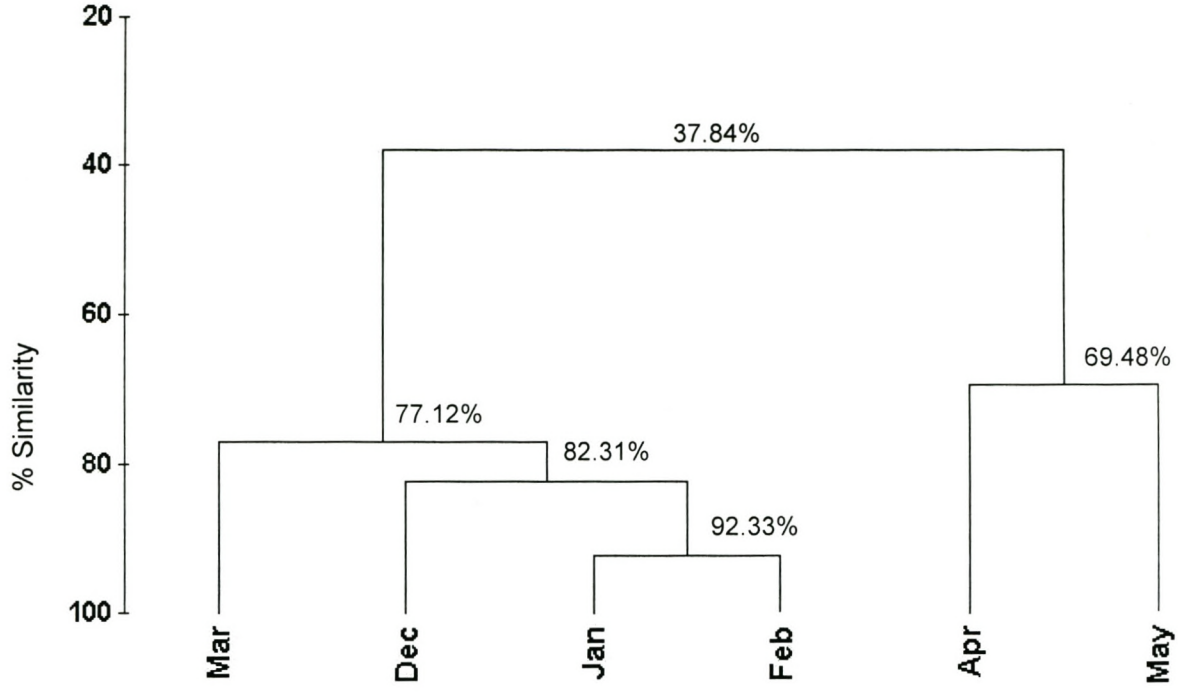


Fig. 14. Hierarchical clustering of months, based on averaged fourth-root transformed Odonata species abundance data.

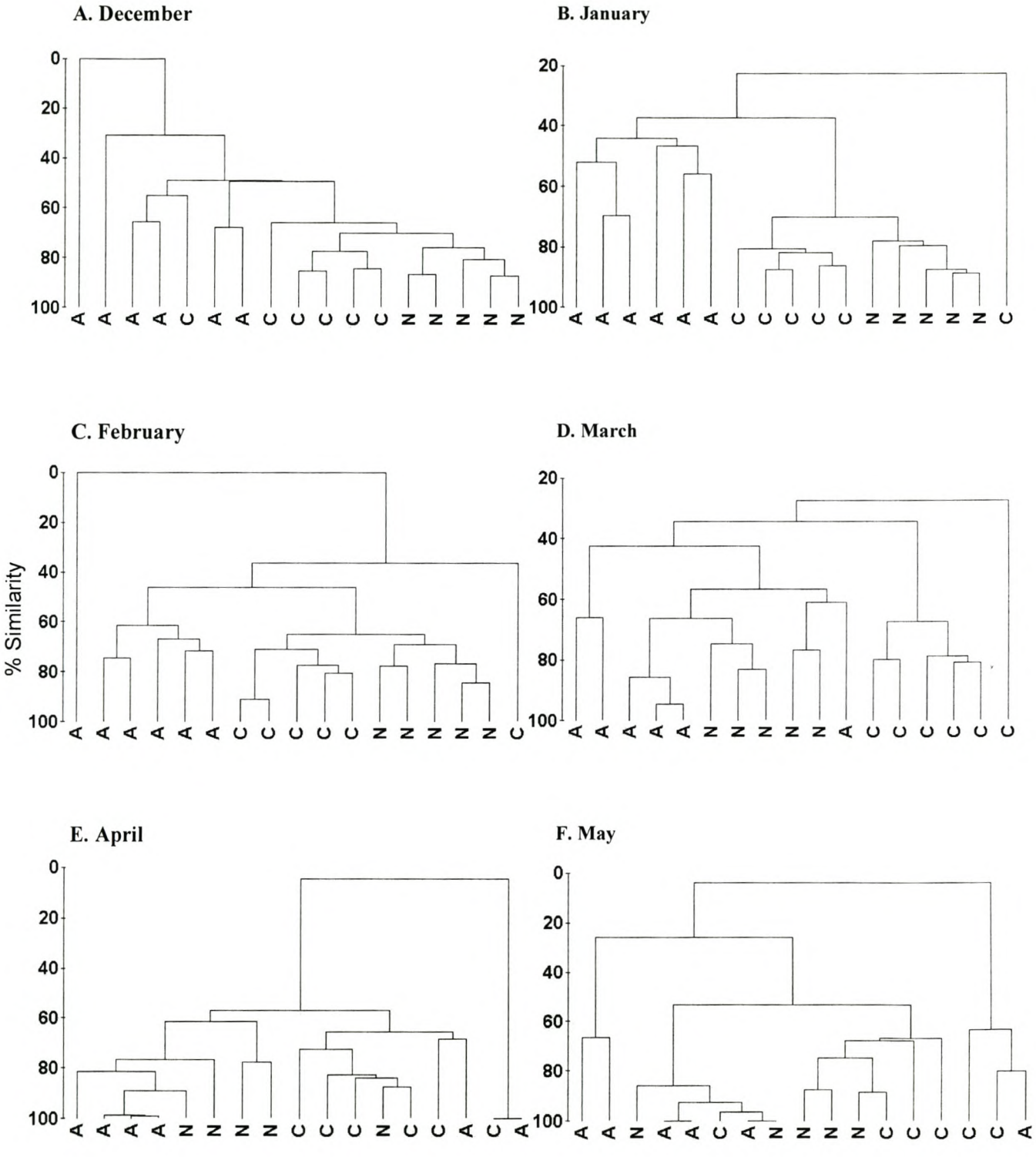


Fig. 15. Hierarchical clustering of cleared, natural and alien sites, based on Odonata species abundance data collected monthly between December 2003 to March 2004 (A-F). A = Alien, C = Cleared, N = Natural.

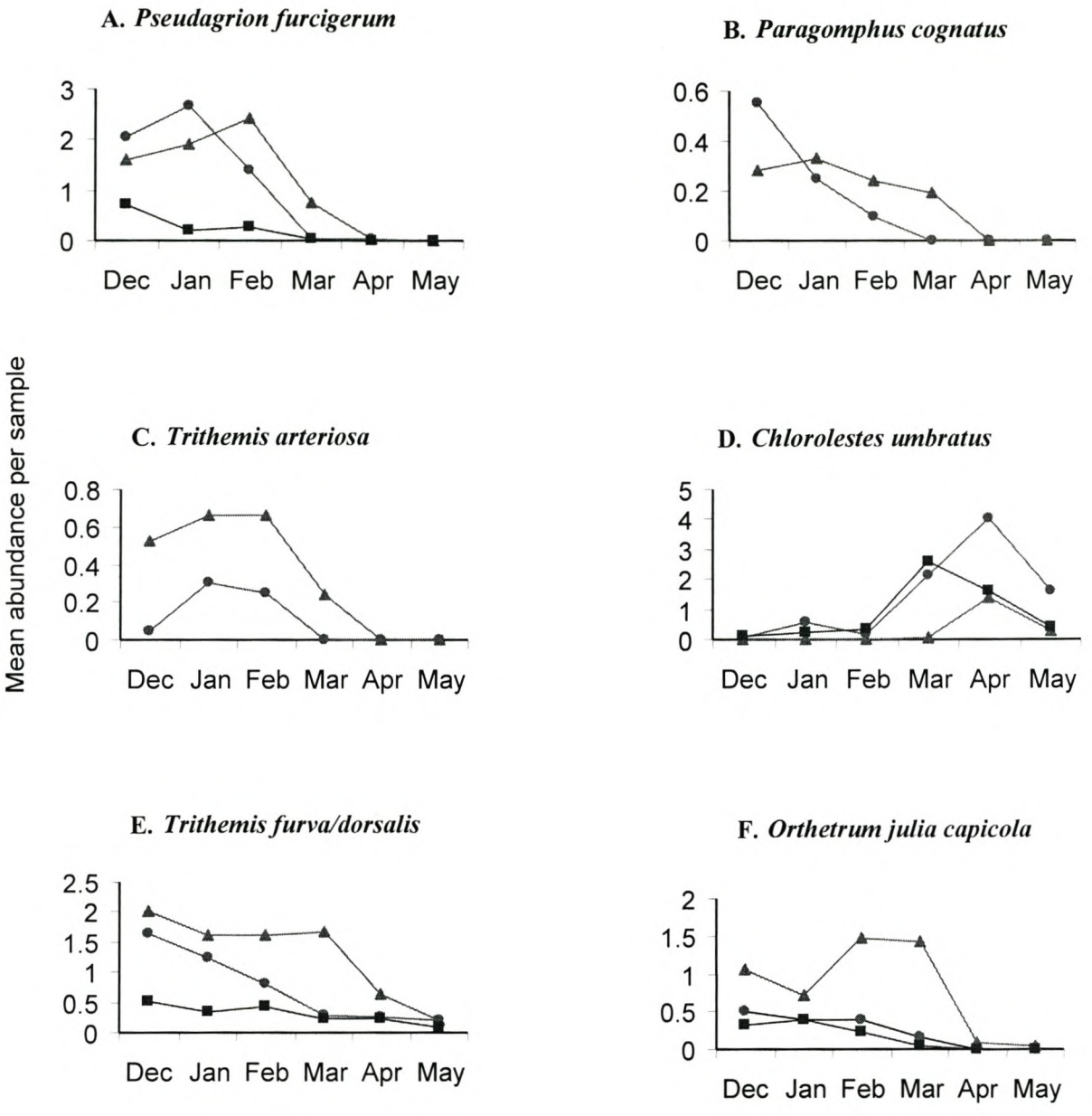


Fig. 16. Seasonal abundance of Odonata species between December and May, showing differences between cleared sites (triangles), natural sites (circles) and alien sites (squares).

0.05 (R = 0.07). March was only significantly different to May (R = 0.66, P = 0.1), while April and May differed significantly (R = 0.519, P = 0.1). ANOVA of species richness and abundance data (Table 3) concurred with the multivariate analyses. In addition, March had significantly lower species richness and abundance than January ($P < 0.05$).

CLUSTER analyses run separately for each month (Fig. 15) show that clearly identifiable assemblage patterns existed for alien, cleared and natural sites between December and March (although somewhat less clearly in March). This grouping broke down in April and May.

In December to February, natural sites were most similar to cleared sites, while in March they were more similar to alien sites. This is because seasonal patterns also differed between alien, cleared and natural sites. Many species declined in abundance in March, this decline often being greater in alien and natural sites than in cleared sites. For example, *Paragomphus cognatus*, *P. furcigerum* and *T. arteriosa* were present in natural sites until March but, in cleared sites, they occurred until April or May (Fig. 16). Conversely, *C. umbratus* was most abundant in shaded alien sites in March but in April and May, it was more common in natural sites, preferring sun-exposed *Prionium* habitats. This species was absent from most cleared sites.

4. Discussion

4.1. Species richness and abundance

In general, an absence of marginal vegetation is associated with lower abundances of larval and adult Odonata (Ormerod *et al.*, 1990; Osborn and Samways, 1996). Moore (1991) observed a decline on Odonata where marginal vegetation died back due to drought, and Clark and Samways (1996) found higher species richness and abundance of Odonata with increasing reed cover. The results of this study are consistent with this pattern. Removal of alien trees caused greater exposure to sunlight and rapid regrowth of marginal vegetation (initially mainly grass and sedge).

This offered a greater array of biotopes, thus supporting a greater number of individuals and species.

The high abundance and species richness in cleared sites suggests post-clearing recovery, while the low abundance in alien sites emphasises the need for further clearing. Natural and cleared sites were generally more similar to each other than to alien sites, confirming that clearing initiates recovery and does not exacerbate disturbance. This is consistent with the intermediate disturbance hypothesis (Connell, 1978; Ward and Stanford, 1983), which predicts maximal species diversity between the extremes of high stress (alien invasion) and complete stability (natural sites). The higher abundance in cleared sites may be a response, not only to the increased availability of biotopes for perching and oviposition, but also to a greater availability of herbivorous prey species attracted to the new plants. However, the higher abundance of adult Odonata in cleared sites does not necessarily indicate breeding success, which can only be confirmed by determining egg and larval survival.

While abundance was significantly lower in alien sites, species richness often matched that of natural sites. This is unexpected, as other studies have generally found diversity to be lower in areas of alien invasion. Donnelly and Giliomee (1985), for example, found a lower diversity and abundance of Formicidae in *Pinus* plantations, while Samways *et al.* (1996) found a lower diversity and species richness of terrestrial invertebrates in invasive alien vegetation.

There are two possible reasons for this discrepancy. Firstly, shading by tall indigenous trees in natural sites may discourage sun-loving species, thus lowering species richness. Secondly, adult dragonflies may tolerate moderate levels of alien invasion or respond rapidly to partial clearing. Partially cleared and lightly invaded alien sites had substantially greater amounts of understorey plants (i.e. grass, sedge, *Prionium* and short fynbos bushes) than highly dense alien sites. Dragonflies appear to respond rapidly to these conditions so that species richness was relatively

high in partially cleared and more sunlit alien sites (several Holsloot, Dwars and Rondegat River sites). This is because the mixture of vegetation types essentially increased the range of plant and sun/shade biotopes available and, hence, the number of species. Therefore, characteristic species in medium-density alien sites included species that are common in cleared and natural sites, such as *T. furva* and *A. speratus*. Dense alien sites were all highly shaded with very little (or no) understorey vegetation and had the lowest abundance and species richness, this being consistent with other studies (Samways and Moore, 1991; Samways *et al.*, 1996). Clearly, even partial clearing can initiate recovery, although larval survival should be assessed to determine the extent of this recovery.

4.2. Environmental influences on species assemblages and implications for conservation

Adult dragonflies are sensitive responders to newly-created physical conditions of both river bank and water (Clark, 1991). Physical and physiognomic conditions generally determine species assemblages in new habitats (Steytler and Samways, 1995). In this study, species distribution patterns corresponded primarily to the physiognomic effects of alien invasion and clearing. Physical factors (conductivity, oxygen, pH, width) largely explained between-river differences. Physical factors may also have affected larval distribution patterns as alien trees and alien leaf litter affect factors such as nutrient content, pH and water chemistry (Johns, 1993).

Plant physiognomy is reportedly more important in influencing invertebrate assemblages than whether the plant is exotic or indigenous (Samways and Moore, 1991; Steytler, 1994; Oelofse, 1996; Samways and Steytler, 1996). Shade has also been found to be more important than alien type (Kinvig and Samways, 2000). This study confirms the importance of shade, which was co-correlated with canopy cover, in influencing species assemblages. Alien type (measured as percentage *Eucalyptus*) was less important.

The importance of sun or shade in species distribution patterns relates to the thermoregulatory requirements of the adults (McGeoch and Samways, 1991). Shade also affects water temperature and thus affects development of larvae and eggs (Ormerod *et al.*, 1990). Sunlight therefore probably signals the suitability of water conditions not visually recognisable to adults (Gibbons and Pain, 1992). Vegetation structure, water depth, width and current probably also act as proximate cues to the potential survival of larvae (Wildermuth and Spinner, 1991).

In this study, species diversity and abundance dropped dramatically in shaded sites, falling to zero in highly shaded dense alien sites. Steytler and Samways (1995) and Kinvig and Samways (2000) found similar results in KwaZulu-Natal. This response to shade appears to be a specific response to invasive alien trees in this country. Elsewhere, such as Mayotte, the response is not as strong, probably because the canopy is less dense or the species are more shade tolerant (Samways, 2004). In this study, only *C. umbratus* was strongly associated with shady conditions between December and March.

Unlike other studies, the most important environmental variable to influence odonate assemblages across alien disturbance regimes was the percentage of the bank's soil exposed to water. This roughly equates to the level of marginal vegetation (particularly understorey macrophytes such as sedge, grass and *Prionium*) covering the banks. Marginal vegetation was conspicuously absent from dense alien sites. The importance of bank exposure, and therefore marginal vegetation, emphasises the role of plant physiognomy in providing perch and oviposition sites. This is consistent with other studies (Oelofse 1996; Samways and Steytler, 1996; Stewart and Samways, 1998). Macrophytes may be important, not only as perch and oviposition sites for adults, but also as nurseries for aquatic invertebrates (Rutt *et al.* 1989; Ormerod *et al.*, 1990; Samways and Steytler, 1996; Stewart and Samways, 1998). The importance of plant physiognomy as a determinant of distribution patterns has been discussed by Samways (1993a) and Steytler and Samways (1995).

At the within-river level, total suspended solids (TSS) was also important. Levels of TSS were above average in cleared and less dense alien sites, suggesting that clearing may result in increased erosion and/or input of organic or inorganic debris. Most likely sources are from the erosion of cleared banks and from plant debris blown or washed into the water during or after clearing. Post-clearing fires may also increase the amount of erodable plant debris and ash along river margins. In addition, greater exposure of cleared sites to wind may contribute to the allochthonous input of debris, as may fires. Of concern, is that this increased TSS may result, not only in greater turbidity of the water, but also modifications to the benthic substrate. Increased turbidity may impede visual predation by larvae, while eroded material may settle to create new sandy or muddy substrates. As larvae often exhibit distinct substrate preferences (Corbet, 1999), these changes may have a considerable effect on species composition.

Unlike other studies (Clark, 1991; Steytler and Samways, 1995; Samways *et al.*, 1996), flow was not of great importance for species distribution patterns. This is because site selection was based on flow regime (i.e. all sites included a pool-run-riffle sequence), in an attempt to standardise data for ease of comparison. Flow rate was only important for *Z. natalensis* which only breeds in fast currents (Pinhey, 1978).

High levels of specificity and preference to vegetation types have been observed in Odonata (Steytler, 1994). Endophytic Zygoptera, in particular, are often closely associated with certain kinds of vegetation (Buchwald, 1992). In this study, distinct species assemblages were identified for each dominant vegetation type: tall indigenous vegetation, short fynbos shrubs, grass, *Prionium* and alien trees (Table 4). Considering the range of biotope preferences of odonates (Fig. 8), it is clear that to maintain biodiversity, a maximum number of suitable biotopes are needed to provide for the biotope requirements of a maximum range of species. Stewart and Samways (1998) found diverse biotopes, created by moderate water level fluctuations, increased Odonata diversity and evenness in the Kruger National Park. Similarly, Steytler and Samways (1995)

found that species richness doubled with the provision of a wide range of biotopes at an artificial lake.

For alien clearing and riparian rehabilitation, increasing biotope diversity would entail maximising the diversity of indigenous plant biotopes (i.e. species and vegetation types) and providing both sunlit and shaded biotopes. The occurrence of some shade may be important on very hot days for temperature regulation. McGeoch and Samways (1991), for instance, reported aggregations of thermoregulating Anisoptera in shaded biotopes. The provision of shade may be particularly important for the rare *C. umbratus*.

Alien clearing appears to initiate a vegetation succession that progresses from grass and sedge to *Prionium* to short indigenous vegetation (Fig. 6). Assemblage patterns appear to follow this succession (Table 4, Fig. 8), so that, for example, *Pseudagrion kersteni* was associated with grassy sites, while *P. furcigerum* was associated with *Prionium* sites and *T. furva/dorsalis* and *E. frenulata* were associated with short indigenous fynbos and *Prionium* sites. *A. leucosticta* was strongly associated with tall indigenous trees. Osborn and Samways (1996) similarly found that variables that represented different ecological successional stages influenced Odonata assemblage patterns at newly colonised ponds. The fact that species assemblages in near-natural (*Prionium*) sites resembled those in cleared sites with dominant *Prionium* growth, suggests that recovery was still in progress at these sites.

Ecological succession is regarded by Usher and Jefferson (1993) as the single most important factor causing change in arthropod communities. Brown and Southwood (1983) found that both abundance and diversity of arthropods increased with successional age of an abandoned arable field, because of the increase in the structural diversity of the plants. The successional stages progressed from 'young field' (primarily grasses) to 'old field' (primarily shrubs) to woodland. Therefore, management of successional stages has often been suggested as a means of

maintaining diversity for insect conservation (Samways, 1994). Donnelly and Giliomee (1985) found that the conservation of biodiversity of Formicidae in fynbos can best be maintained by a staggered burning regime. For Odonata, staggered felling of commercial forestry trees has been suggested to maintain species diversity along rivers (Oelofse, 1996; Samways and Steytler, 1996). Clearly, rehabilitation of cleared river margins in the Western Cape should aim to encourage this vegetational succession to increase biotope diversity and therefore species diversity.

Further biotope heterogeneity can be created by maintaining plants at a range of ages (i.e. heights) as the existence of different plants and perch heights may enable species packing (Sternberg, 1994). For instance, Steytler and Samways (1995) found that the distribution of different species of Odonata correlated with different lengths of grass and Usher and Smart (1988) found that spider diversity can be maintained by a mosaic of differently-aged heather. The range of perch heights may also facilitate thermoregulation, allowing species to perch high on hot days and lower on cold days (McGeoch and Samways, 1991).

Alien clearing appears to affect the seasonal and diurnal activity patterns of adults, extending the season of activity for species such as *T. arteriosa* and *P. cognatus*. Greater exposure of the river to sunlight may increase the thermal energy available for flight, mating and oviposition. There may also be an increase in the growth and maturation rates of tenerals. According to May (1991), if body temperatures are maintained above a certain level, adult fecundity may be increased because the period of spermatogenesis is extended and the period of egg maturation is reduced. Altered water temperatures may also affect larval development and survival rates, thus affecting emergence times and, ultimately, fluctuations in species composition over time (Stewart and Samways, 1998). Alien invasion and alien clearing may therefore have profound effects on the abundance, distribution and survival of species. Increased exposure to sunlight in cleared sites may, for instance, increase the reproductive success of certain sun-loving species but decrease the survival of species that require shade for thermoregulatory purposes.

4.3. Endemic species

Biodiversity management needs to consider, not just number of species, but also processes. It should therefore consider factors such as whether species are endemic and stenotopic or widespread and eurytopic (Samways, 1994). It is not the highly mobile migrant species but the highly residential species that are, arguably, the most important for conservation and are most likely to be valuable indicators (Samways, 1993b). Species with extremely restricted geographical ranges are often the most vulnerable to disturbance (Samways, 1994). Therefore, the relative proportions of endemic versus widespread species can often be used to make conservation decisions regarding rarity, endemism or typicalness (Samways, 1993b).

Widespread eurytopic species are usually the first to colonise new habitats (Usher and Jefferson, 1993). Davis (1989) found that 'ubiquitous' butterfly species rapidly colonised a landfill site, while the local species had to be translocated from other areas for active reintroduction. This is consistent with newly cleared riparian habitats. *T. furva/dorsalis* and *A. speratus* are widespread eurytopic species (Samways and Steytler, 1996) common in cleared and natural sites and even occurring in several alien sites (Table 1, Fig. 8). They were most dominant in newly-cleared grassy sites (Table 4, Fig. 8) and less dense alien sites, being the first to colonise these 'new' habitats. Also abundant in cleared grass- and *Prionium*-dominated sites were *P. kersteni*, *T. arteriosa* and *C. sanguinolenta* (Table 1, Fig. 8), all widespread eurytopic species (Clark, 1991; Samways, 1991). This was also observed by Steytler and Samways (1995). These eurytopic, widespread species also occur in regions where grass and reeds are the dominant riparian vegetation and they are therefore easily able to adapt to newly-cleared grassy conditions. Encouragingly, these cleared sites also had an abundance of *O. julia capicola* and *P. furcigerum* (Tables 1 and 4, Fig. 8), both endemic species, suggesting that clearing may actually benefit these species.

Consistent with the findings of Samways and Steytler (1996) and Oelofse (1996), most of the eurytopic species in grass-dominated sites were Anisoptera and a few widespread, eurytopic Zygoptera. Unlike libellulid Anisoptera, the Zygoptera are mostly endophytic (Corbet, 1999) and may be more stenotopic and therefore more affected by changes in vegetation type.

While clearing initiates a fairly rapid recovery of grass and recolonisation by eurytopic sun-loving species (thus increasing abundance and species richness), this does not necessarily imply recovery in terms of overall biodiversity. Effective biodiversity conservation also needs to provide the habitat requirements of stenotopic, endemic species (mostly Zygoptera). The endemic Western Cape zygopteran, *P. furcigerum* was common in *Prionium*-dominated sites (Table 4, Fig. 8). *C. umbratus* was also observed to be strongly associated with *Prionium* and short fynbos from mid-March onwards. (This was not reflected by the data, which excluded April and May.) The endemic *A. leucosticta* was common only in tall indigenous sites, while *E. frenulata* (which also occurs in Angola) was associated with short indigenous fynbos and *Prionium*. Therefore, for recovery in terms of overall biodiversity, the recovery of indigenous bushes (essential for *C. umbratus*, *A. leucosticta* and *E. frenulata*) and *Prionium* (preferred by *P. furcigerum*) is essential for endemic species.

The removal of alien vegetation may increase diurnal and seasonal fluctuations in temperature through greater exposure of the river and its banks to sunlight. In addition, exposure to inclement weather conditions (e.g. wind or rain) and predation may increase. Consequently, life history strategies and survival rates may be affected. Wilson and Yoshimura (1994) considered temporal climatic variation to favour the fitness of generalists relative to specialists and Clark (1991) found a dominance of *T. arteriosa*, a eurytopic species, in sites with water fluctuations. In this study, eurytopic species were more dominant in exposed, cleared sites, apparently confirming that greater temperature fluctuations in cleared sites favour eurytopic species, while stenotopic and endemic species may actually be deterred by this instability.

Clark (1991) suggested that the stability of a river can be indicated by the relative proportions of eurytopic to stenotopic species. Since most Anisoptera recorded here are eurytopic and most Zygoptera are stenotopic, their relative proportions may add insight into the extent of post-clearing recovery or disturbance.

4.4. Rare species

C. umbratus is nationally Red Listed as Near Threatened (Samways, 2005) and is threatened primarily by alien trees and habitat loss (Samways and Taylor, 2004). Surprisingly, this species, together with the endemic *O. julia capicola*, characterised dense alien sites in this study. The natural habitat preference of *C. umbratus*, at least between December and March, is dense indigenous forests and it appears that, where these habitats are absent, they have adapted to *Acacia* forests. Where this species was found outside of alien vegetation between December and February, it was always associated with dense indigenous trees in natural sites. Oelofse (1996) found *Chlorolestes tessellatus*, a species with similar biotope preferences to *C. umbratus*, to occur only in shaded indigenous forest sites in KwaZulu-Natal, but it was absent from sites with alien *Eucalyptus* trees. This may be a response to vegetation architecture as *Eucalyptus* trees are generally taller and therefore not as closely connected to the water as *Acacia* trees. A similar response to vegetation architecture has been found in the aggregation behaviour of butterflies on hilltops (Lawrence and Samways, 2002). Here the response was to vegetation structure relative to the amount of sunlight reaching the forest floor, and not to the tree species itself, so that shaded dense alien and shaded natural forest sites were both devoid of butterflies.

C. umbratus is shade tolerant (Samways and Steytler, 1996) and can survive under alien canopies with sun shafts (Samways and Taylor, 2004) so that the trees *per se* are not a major threat. However, the trees shade out the understorey so that there is little growth of grass, *Prionium* and small bushes, thus reducing the number of favourable perch sites (*Prionium*) and oviposition sites

(bushes) (Samways and Taylor, 2004). In dense alien sites, *C. umbratus* perched on the *Acacia* trees themselves but their ability to oviposit and breed successfully is questionable and is probably limited to sites with indigenous fynbos elements. A survey of larval populations in these sites would confirm this.

While alien trees are threatening the survival of this rare endemic species, the removal of *Acacia* trees does not appear to be of immediate benefit. *C. umbratus* was infrequently encountered in cleared sites, probably because of a lack of *Prionium*, indigenous bushes and shade. Its occurrence in near-natural sites, however, suggests that longer-term recovery is possible, providing there is access from a nearby source population. According to Kinvig and Samways (2000), *C. tessellatus* requires the thermal balance provided by the 'right combination' of sunlight and shade and the growth of understorey plants (i.e. bushes and grasses). Samways and Steytler (1996) recommended that felling of forest trees be staggered over time so as to minimise the disruption of these conditions. It may be that *C. umbratus* requires a similar approach during alien clearing to minimise the sudden loss of shaded conditions, while simultaneously replacing the removed trees with *Prionium* and fynbos perch and oviposition sites. This also reinforces the importance of prioritising newly-invaded and less-dense sites for alien clearing.

Alien trees may act as a barrier to *C. umbratus* movement, preventing them from colonising cleared or natural sites. Alien trees act as a barrier to the movement of *Lestes barbarus* in Europe (Hill *et al.*, 1999) and to butterflies in South Africa (Wood and Samways, 1991) and may be an important consideration in the conservation of *C. umbratus*. Cleared sites may also act as a barrier to movement if there are no suitable perch sites and inadequate shade.

Of further concern is that alien trees may affect populations by shortening the season of activity. *C. umbratus* declined sharply in abundance in alien sites in April, while remaining fairly common

in natural sites throughout April and May. The effect this has on breeding success and population fluctuations bears further investigation.

4.5. Indicator species

Biotopes shared many species so few indicator species were identified. This is consistent with Samways and Steytler's (1996) findings from urban and cultivated forest riparian zones. *A. leucosticta* was the only species that could consistently be regarded as an indicator species for natural conditions with tall indigenous trees as dominant vegetation type. This is primarily a response to vegetation type, rather than to shade, as the species was generally absent from alien sites. In KwaZulu-Natal, Oelofse (1996) and Samways *et al.* (1996) also found this species to be highly associated with forest biotopes with much shade and many bushes, being most abundant in sites with the least alien vegetation.

A. leucosticta would be useful for identifying fully-recovered cleared sites or undisturbed natural sites. A site can be considered fully recovered when the incidence and abundance of *A. leucosticta* equals that of natural sites. Conversely, a low incidence and abundance of *A. leucosticta* would indicate a lack of recovery of cleared sites or a disturbance in natural sites (such as alien invasion, removal of indigenous trees or fire). This species is highly suited as indicator species as it is conspicuous, easily identified in the field, relatively abundant in natural conditions and is a stenotopic endemic species, thus being very sensitive to habitat changes (Samways *et al.*, 1996).

A. leucosticta was not completely absent from cleared sites where it was usually associated with short indigenous vegetation. Isolated individuals even occurred in the more open alien sites. Because of this biotope overlap, relative abundance data would need to be carefully analysed. For effective monitoring, it would be essential to know baseline population levels, either historically or from careful selected natural sites.

P. furcigerum is a potential detector species in near-natural sites with extensive growth of *Prionium*. This species also had high indicator values in cleared sites with prominent *Prionium* stands. Therefore, where *Prionium* recovers after clearing, *P. furcigerum* will increase in abundance and incidence. Conversely, this species will decline in abundance and incidence with decreasing *Prionium* growth. It should be noted, however, that this decline may signify decreased *Prionium* growth both as a result of alien invasion and of indigenous tree recovery (Fig. 9). Shade from indigenous trees also reduces *Prionium* growth. This species will therefore be very useful for monitoring the early stages of clearing, while *A. leucosticta* would be more useful for detecting recovery of indigenous trees. *P. furcigerum* is a very local species endemic to the Western Cape. It is therefore of conservation importance and is highly suitable for monitoring purposes.

This study only looked at one river with extensive *Prionium* growth (Witte River) and also grouped together all cleared sites, irrespective of the extent of *Prionium* growth. Further research will be useful to confirm the population trends of *P. furcigerum* in cleared sites with successive levels of *Prionium* recovery.

In summary, where *A. leucosticta* indicates indigenous tree recovery, *P. furcigerum* detects *Prionium* recovery. Of the two, *P. furcigerum* is potentially more useful for monitoring alien disturbance as it will track the recovery/invasion process with a gradual increase or decrease in abundance and incidence. It will also track the direction of change, i.e. increase or decrease in response to recovery or deterioration. *A. leucosticta* will be useful to indicate recovery, but its greatest potential lies in the field of biodiversity conservation as it could be very useful in identifying high-priority areas for conservation action and for protection from alien invasion.

The applicability of these species for monitoring is restricted to the months of December, January and February in the middle reaches of Western Cape rivers. Further research during November

and October could extend this monitoring period. If monitoring were to occur in March or April, the only potential indicator species is *C. umbratus* in near-natural sites. However, this result was derived from a single river and would require further testing. The general applicability of *A. leucosticta* and *P. furcigerum* as indicator/detector species should also be tested across rivers, zones, geographic regions and years.

4.6. Recommendations for clearing and rehabilitation

Vane-Wright (1993) predicts that the 21st century will be known as the age of restoration biology, as we attempt to find ways to maintain biodiversity and ecosystem services. The study of restoration of rivers is in its infancy and more studies in this regard would go a long way to achieving biodiversity objectives. Conservation objectives of any rehabilitated habitat often focus on 'structural restoration endpoints', such as species richness and diversity (Muotka and Laasonen, 2002), rather than the restoration of ecosystem processes ('functional endpoints'). In fact, restoration objectives should be based on both structural and functional components. If the functional integrity can be restored then an increase in biodiversity will follow (Downes *et al.*, 2002). This can only be achieved by habitat management (Usher and Jefferson, 1993) and requires knowing the habitat requirements of target species (Downes *et al.*, 2002).

Adult Odonata, being highly mobile, are known to be rapid colonists of newly created pools (Usher and Jefferson, 1993). Similarly, recently cleared river margins rapidly attracted several widespread eurytopic species. However, to conserve biodiversity, rare and local species also need protection. This requires the provision of their preferred *Prionium* and fynbos biotopes. Unfortunately, recovery of these plants can be a lengthy process, particularly in areas where alien density was high for many years (e.g. Witte River cleared sites). As Zavaleta *et al.* (2001) point out, eradication alone may not allow ecosystems to recover, as invaders may modify the habitat, rendering it unsuitable for native species. Eradication goals should therefore be integrated with

restoration goals. Restoration of sites for insect conservation is associated with the 'plantscape' in which the insects live (Samways, 1994). Clearly, there is a need to re-plant and cultivate indigenous riparian plants in cleared areas, while simultaneously removing regrowth of alien seedlings.

In general, the aim should be for biotope heterogeneity to support both eurytopic and stenotopic, endemic species. This heterogeneity can be created by: (1) partial or staggered clearing over time or space (possibly with staggered clearing alternating between banks), thus allowing for the recovery of some indigenous vegetation that can maintain populations once the remaining trees are cleared; (2) simultaneously planting indigenous seedlings of different successional stages (i.e. *Prionium* and fynbos shrubs), species and ages (i.e. heights); and (3) not using the 'fell and burn' method as this has the greatest negative effect on guild survival (Holmes *et al.*, 2000). The 'fell and burn' treatment, as opposed to the 'burn standing' or 'fell, remove and burn' treatments, result in highly intense fires and only non-mycorrhizal graminoids tend to persist. Holmes and Marais (2000) also suggest post-fire sowing to accelerate vegetation recovery in areas that had been heavily invaded for long periods, as well as anti-erosion measures to prevent seed-banks from being washed away.

These measures would offer a greater variety of perch and oviposition sites, thus catering for a larger number of species, especially stenotopic, endemic species. *C. umbratus*, in particular, would benefit from staggered clearing and recultivation of indigenous plants, both of which would provide perch and oviposition sites as well as partially shaded habitats. Biotope heterogeneity would also potentially attract a larger number of prey species, thus supporting a greater abundance of Odonata and other predators.

It would be an obvious advantage to target lightly invaded alien sites for clearing, as existing indigenous vegetation in these sites can be maintained, pre-empting the need for planting. Seed

banks should also be maintained and sites with healthy indigenous seed banks and deep soil should be prioritised.

In most cases, grass grows fairly rapidly after clearing. However, in this study, there was one noticeable exception. Along sections of the Rondegat River, the banks were very steep and exposed with very little vegetational recovery. Here percentage exposed banks and grass/sedge had high correlations with assemblage patterns. This, together with the clear importance of suspended solids as a factor influencing species distribution patterns, further emphasises the importance of anti-erosion methods. Vegetational recovery can be assisted by using sediment traps or flow deflectors and bank stabilisation methods (e.g. gabions or pioneer grass species) (Downes *et al.*, 2002). Cultivation of *Prionium* will also assist in bank stabilisation. It may also be necessary to consider soil management methods as alien trees have a direct effect on the physical properties of the soil and this further impedes regrowth of indigenous vegetation. Pienaar *et al.* (2003) suggested flushing of sediments, although this may affect larval populations. There is clearly a need to establish what effect increased suspended solids (with possible substrate and turbidity changes) have on larval populations.

It is generally far more expensive to rehabilitate an ecosystem than to prevent disturbance in the first place (McNeely *et al.*, 1995). Remembering this, Working for Water should consider protecting highly biodiverse rivers from alien invasion, even if just to keep river corridors free of aliens. In so doing, ecological integrity and ecosystem services will be maintained. It would be useful to assess the number of rare, endemic (*C. umbratus* and *P. furcigerum*) and indicator species (*A. leucosticta*) as a means of identifying areas for protection. A high abundance of these species would indicate the need for conservation effort. A complementary method would be to assess the incidence and abundance of *A. leucosticta*, *A. subpupillata* and *E. frenulata*. Where these three species co-occur in most of the sites, natural conditions are indicated and these could be prioritised for protection.

Ecological restoration is often linked to landscape ecology (Bell *et al.*, 1997). Alien clearing programmes should therefore consider landscape criteria such as patch size, configuration and corridors for movement to facilitate the recruitment of invertebrate species. The likelihood of a species becoming re-established in a cleared area depends on the proximity of the area to suitable source populations that are able to disperse to it.

Where possible, extinctions from individual catchments should be avoided as dispersal across catchments is usually more difficult because of larger distances. Recolonisation generally occurs from source populations along the same river (Zwick, 1992, Morely and Karr, 2002). Zwick (1992), for example, found that relic populations of Plecoptera are unlikely to recolonise rivers where they have become extinct.

Landscape ecology is rooted in the island biogeography theory (Mac Arthur and Wilson, 1967). If the distance between populations in habitat patches is too great, these habitats become islands. With no immigration from other suitable habitats, biotic diversity is reduced in the island patch and extinctions can eventually occur. The rate of extinctions is largely determined by the size of the patch, its shape, configuration, distance from, and connectivity to, other populations (Bell *et al.*, 1997). Corridors for movement and patch sizes are therefore often considered in the construction of reserves (Wiens, 1995).

Often, dispersal ability is a key factor affecting population fluctuations in habitat patches (Dempster, 1991). Zygopterans, many of which are stenotopic endemics, tend to be poorer fliers than the more eurytopic Anisoptera and are therefore more prone to isolation and fragmentation. Purse *et al.* (2003), for example, found the rare and specialised european damselfly, *Coenagrion mercuriale*, to be a poor disperser. Mature adults had low rates of movements within habitat patches (less than 25 m), low rates of emigration (1.3-11.4%) and colonisation (maximum 1 km) and dispersal was considerably reduced by barriers of scrub. In South Africa, it is likely that alien

trees also act as a barrier to movement, thus impeding recolonisation. In Wales, conifer trees are known to impair the foraging behaviour of *Cordulegaster boltoni* (Ormerod *et al.*, 1990) and this may be why *Anax imperator* was seen here to fly over, but not through, *A. mearnsii* stands to reach the next stretch of open river. Cleared sites could also act as a barrier to movement if they do not provide suitable conditions for perching or oviposition. This may be the case for *C. umbratus*, which was virtually absent from cleared sites. Clearly, the dispersal abilities of adult Odonata through alien or cleared areas bears further investigation and isolation of populations by alien trees (or cleared areas) should be avoided.

Once the dispersal abilities of dragonflies are understood, minimum patch sizes and corridor requirements can be established to guide conservation management decisions regarding clearing or protection of riparian vegetation. Until such time, large fragments of natural patches should be targeted for protection, and movement corridors should be maintained to facilitate recolonisation of both natural and cleared patches.

Where alien trees are found to act as a barrier to movement of rare or endemic species, it would be worth considering clearing patches of alien trees at regular intervals along the length of the river (e.g. staggered clearing of one bank at, say 20 m intervals). This would provide 'stepping stones' for migration, allowing for recolonisation of areas where there may have been local extinctions. For this to be effective, the dispersal abilities and habitat requirements need to be ascertained for the target species. For instance, Haddad (2000) found that, for the butterfly, *Junonia coenia*, patch colonisation was equally efficient via stepping stones and corridors at small distances, but as distances increased, corridors became more effective. He concluded that when distances are short compared to an animal's movement ability, a stepping stone approach may be most effective to promote dispersal. However, at longer inter-patch distances, corridors have higher conservation value. Purse *et al.* (2003) recommended that, for the conservation of *Coenagrion mercuriale*, small habitat patches that are close to large core sites (containing source

populations) be protected, and any barriers of scrub between patches be removed to facilitate stepping stone-like dispersal movements.

However, Rosenberg *et al.* (1997) warn that, while corridors may facilitate dispersal, the extent to which they maintain biodiversity and prevent local extinctions remains uncertain. Therefore, while it may reduce fragmentation of populations, it cannot be used in isolation as a conservation tool. It is generally agreed that conservation should consider the entire catchment, rather than just riparian zones (e.g. Morely and Karr, 2002; Saunders *et al.*, 2002). Willson and Dorcas (2003), for example, found that stream salamander populations were effectively conserved by considering land use throughout the catchment, rather than by just preserving small riparian buffer zones. As Noss (1991) points out, connectivity of process is just as important as connectivity of habitat.

4.7. Recommendations for monitoring

To gauge the effectiveness of habitat rehabilitation and to manage the clearing programme according to sound conservation and ecological principles, a monitoring programme should be implemented. Several recommendations are made in this regard and these should be communicated to reserve and project managers. Monitoring will help to identify key issues and prioritise areas for clearing or protection according to biodiversity conservation objectives. It can be used to inform policy-makers and guide management decisions (Stork and Samways, 1995). The *Global Biodiversity Strategy* (WRI/IUCN/UNEP, 1992) recommends monitoring as an 'early warning system' to detect potential threats to biodiversity and take preventative action. Considering the expense of alien clearing, it would be financially advantageous to identify threats from alien invasion early enough to take preventative, rather than corrective action. Monitoring would also detect inappropriate management actions, such as harmful clearing methods.

Monitoring involves the "intermittent surveillance (regular or irregular) to ascertain the extent of compliance with a predetermined standard or the degree of deviation from an expected norm"

(Hellawell, 1991). Species assemblages can be used to initially identify biotopes, while rare, endemic and indicator species can be used to provide specific information for conservation priorities and management decisions.

Characteristic species assemblages were identified for each disturbance regime (Tables 4 and 5), providing river managers with the means to rapidly classify biotopes and assess changes in physical conditions (such as changes in successional stage from grass-dominated to *Prionium*-dominated cleared sites). It is important to note, however, that species assemblages only indicate the physical and vegetational state of the river and not the cause of that state. That is, disturbance from other sources (e.g. fires, pollution) should be ruled out before interpreting conditions in terms of alien invasion or removal. These species assemblage patterns are only relevant to the middle reaches of Western Cape rivers between December and March. The relative proportions of narrow endemic and widespread eurytopic species may also give an initial indication of the level of post-clearing recovery.

The incidence and abundance patterns of *A. leucosticta*, *A. subpupillata* and *E. frenulata* may be of particular value for initial riparian zone assessments. Where these three species occur together in most of the sites (between December and March), natural vegetation is likely to prevail. In cleared sites, *A. leucosticta* can be expected to be largely absent, while, in alien sites, no more than one of the three species can be expected to occur in any given 15 m site. While *A. leucosticta* appears to have a specialised preference for indigenous trees, *A. subpupillata* and *E. frenulata* can also be expected to be abundant in sites with a range of other vegetation types, but always being most abundant in indigenous vegetation. They can therefore be expected to be fairly common in recovering cleared sites, with *E. frenulata* often being closely associated with *Prionium*. These patterns of incidence and abundance may provide an initial indication of the extent of recovery of indigenous riparian vegetation. In addition, these species may prove to be useful as

complementary species, in conjunction with rare, endemic and indicator species, to identify areas worth conserving.

To monitor specific responses to alien invasion and clearing, *A. leucosticta* and *P. furcigerum* are potentially useful indicator and detector species. However, their reliability needs to be tested in different rivers with different flow regimes over several years to ensure they are geographically and temporally robust as indicators (McGeoch, 1998). If the relationship with disturbance regime is maintained, a standardised monitoring protocol should be established. This would start with an initial assessment of the abundance of *A. leucosticta* and *P. furcigerum* in natural areas. Then, once clearing commences, population levels would be assessed at least once a month between December and February in both cleared and natural areas. A decline in abundance of *A. leucosticta* in natural areas would indicate increased alien invasion. An increase or decrease in the abundance of *P. furcigerum* in cleared areas would indicate recovery or decline in *Prionium*, remembering that an eventual decline in abundance will occur when indigenous trees recover. At this stage the abundance of *A. leucosticta* will increase until, finally, its abundance in the recovered cleared area equals that of the natural area. This means of assessing recovery or disturbance would be both quick and cost-effective.

Whether using indicator species or species assemblages of Odonata, more than one sampling occasion is required for accurate assessments, to counter the effects of seasonal variations (Hawking and New, 2003). Schmidt (1985) suggests that environmental appraisals should span three to five recording days to eliminate irregularities from uncharacteristic species. A minimum of eight sites per month (per disturbance regime) is recommended to ensure that most species are sampled. This is based on the cumulative curves for species, which had reached their asymptotes after 25 samples. Rivers with very high species richness may require more sites to sample all species. To prevent pseudoreplication, it is also recommended that different sites are randomly selected on each visit and no sites sampled on consecutive visits.

Because of the overlap between biotopes (e.g. *A. leucosticta* was present in a few cleared and alien sites), the interpretation of relative abundance data must be done with caution. It is also essential to select reference conditions carefully for accurate comparisons.

It is also advisable to monitor population levels of stenotopic and endemic species to detect threats to rare and specialised species (Samways, 1994). *C. umbratus,* in particular, should be monitored. Its recovery is expected to coincide with the recovery of *Prionium* and fynbos, assuming source populations are close enough for recolonisation. This species should be assessed in April and May when they are most abundant. However, as a relatively rare species, greater sampling effort may be required to get accurate counts.

One could argue that monitoring of vegetation biotopes, such as grass, *Prionium*, fynbos shrubs and indigenous trees, would be more practical than monitoring dragonfly species. However, the presence of suitable plant biotopes is no guarantee that endemic or rare dragonfly species are present, thus still requiring additional population monitoring. Nevertheless, as adult dragonflies are only able to be monitored in summer, it may be prudent to complement these data with vegetation assessment using the Riparian Vegetation Index (Kemper, 2001) in conjunction with water quality assessment using SASS5 (Dickens and Graham, 2002) at other times of the year.

Odonata cannot, on their own, accurately evaluate environments for sound conservation decisions (Samways, 1993b). They are most useful as indicators with complementary taxa, as this will 'increase the depth of the biodiversity picture' (Samways, 1993b, 1994). As top predators, they are most useful in congruence studies with other functional groups, particularly herbivores, as this provides a clearer assessment of ecosystem function, and not just structure (Samways, 1994; Williams, 1997). This would detect, for example, an outbreak of herbivores because of slow colonisation by predators to new habitats (Williams, 1997). Samways (1993b) suggests that Odonata distribution patterns be compared with those of Ephemeroptera to determine impacts on

a stretch of river, with Coleoptera to determine landscape fragmentation or restoration effects, or with birds and butterflies to determine biodiversity effects. Samways (1993b) also suggested that Zygoptera, in particular, be used in congruence studies alongside lycaenid butterflies, for recognition of areas high in endemism. However, for a rapid assessment of alien disturbance regime, single species indicators, in conjunction with species assemblage information, would still provide valuable information for alien management decisions.

4.8. Recommendations for future research

The rate of recovery was not investigated in this study. Considering the expense of rehabilitation work, it would be useful to determine natural (unassisted) recovery rates under different scenarios. Rehabilitation methods can then be used that match the recovery potential. Sites that were cleared more than two years ago should therefore be investigated.

According to King and Schael (2001), each river and each catchment is unique (i.e. signature rivers and catchments). In this study, differences between rivers (72% similarity) did not mask odonate assemblage patterns according to disturbance regime. It therefore provides a good starting point for further, more specific studies in other rivers, other catchments and other zones, perhaps including the months of October and November. Moreover, the usefulness of *A. leucosticta* and *P. furcigerum* as indicator and detector species needs to be extensively tested, and the geographical limits to the applicability of these findings should be determined.

The comparison between CA and CCA solutions indicated outstanding environmental variables. Scale of sampling may have been a contributory factor. Future studies could fine-tune both the scale of the study and the environmental variables measured. As assemblage patterns tended to reflect biotopes, the scale of sampling may have resulted in conflicting effects between biotopes within each site. It may be more effective to look at species abundance patterns at a biotope level (e.g. *Prionium*, grass, boulders, sun, shade, etc.), rather than along a particular stretch of river.

This will elucidate specific responses, such as a direct response to sunlight, as opposed to a response to marginal vegetation. This may explain, for example, why a potential indicator species (*A. leucosticta*) is occasionally encountered in alien and cleared sites. Biotope complexity (e.g. the number of plant species present) should also be measured as this is reportedly correlated to species richness in newly colonised ponds (Osborn and Samways, 1996).

The effect of predatory alien fish such as trout and bass on larval dragonfly populations is largely unknown but this could well intensify the threat to endemic and rare species. There is evidence of this in the Witte River where the globally Red Listed *Ecchlorolestes peringueyi* (Samways, 2002) is found only above waterfalls, out of reach of trout (Samways and Taylor, 2004). In this study, alien fish were present in all rivers except the Rondegat River. It would be useful to determine the compounding effects of, not only alien fish, but also factors such as trampling by cattle, erosion of exposed banks, nutrient-enrichment from farm runoff, abstraction and impoundments, the chemical effects of alien leaf decomposition and the potential threats of global warming on rare and endemic species.

Alien trees and their removal cause temperature changes which, in turn, may affect species composition, growth rates, activity patterns and emergence times and, ultimately, species distribution patterns (Stubbs and Warren, 1991). Clearing may also increase temperature fluctuations and exposure to inclement weather and predators. There is a need to understand how these temperature changes affect seasonal activity, breeding success, life history strategies and survival of both adults and larvae and, in particular, endemic and rare species.

The presence of adults at a water body does not necessarily mean successful larval survival at that site (Oelofse, 1996). For instance, *Pantala flavescens* often oviposits in artificial pools with very poor breeding success (Samways and Caldwell, 1989). Selection of oviposition and breeding sites by adult Odonata is largely visual (Corbet, 1999). However, their survival and distribution is

ultimately determined by water, vegetation and substrate conditions for egg and larval development (Pinhey, 1978). Larvae are often also biotope specific and may be similarly affected by vegetation patterns (Samways, 1993b), possibly compounding the effect of alien invasion and clearing on adult distribution. Therefore, for a fuller understanding of the effects of alien disturbance, larval assemblages need to be assessed. Where adult assemblages provide information on riparian habitat condition, larvae may provide information on water quality and aquatic habitat condition.

There is a need to understand the severity of landscape fragmentation and population isolation resulting from alien trees and their removal. This will depend on dispersal abilities across an alien invaded and cleared riparian landscape. There is evidence that isolation of populations of the swallowtail butterfly, *Papilio machaon*, is accompanied by reduced mobility (Dempster, 1991). Clearly, knowledge of dispersal abilities, the effects of isolation and the ability of endemic Odonata to recolonise cleared habitats, is essential for the formulation of conservation management strategies.

Odonata, as conspicuous top invertebrate predators with wide home ranges, are highly suited as a flagship group for conservation decisions regarding a range of other taxa (Samways, 1993b). However, how representative are they? If their distributional responses to vegetational changes along rivers are reflected by similar responses in other taxa, they would be more useful as indicators (McGeoch, 1998). Further research should determine how representative the Odonata are and how representative the two indicator species are of other endemic species.

5. Conclusion

These results bode well for the Working for Water Programme. Abundance, species richness and biodiversity of Odonata in cleared sites resemble those of natural sites, indicating recovery. In

terms of species distribution patterns, there were also clear signs of recovery. Recovery appears to be relatively rapid, with even partial clearing of alien stands having a marked effect.

However, the main beneficiaries are widespread African species. Therefore, to conserve and restore biodiversity and to protect rare, endemic species, such as *C. umbratus*, there needs to be a shift in emphasis from strict alien clearing to a broader ecosystem restoration goal. It is recommended that active protection, rehabilitation and monitoring be integrated into the Working for Water Programme. More specifically, Working for Water needs to: (1) rehabilitate the natural vegetation, aiming for biotope heterogeneity and plant diversity that will cater for stenotopic and eurytopic species; (2) work with conservation planners to protect highly biodiverse areas from alien invasion; (3) prevent fragmentation and isolation of populations along catchments and optimise recolonisation potential and (4) assess and monitor rivers using odonate assemblages, together with rare, endemic and indicator species, to evaluate post-clearing recovery and to identify areas for protection or clearing on an on-going basis.

This study has shown that adult Odonata provide a rapid and cost-effective means of assessing alien disturbance regime. They are particularly useful for prioritising areas for biodiversity conservation, as well as for evaluating clearing and rehabilitation efforts. Their usefulness will be further enhanced if used in conjunction with other biotic groups, such as benthic macroinvertebrates and riparian vegetation.

References

Allan, J.D., Flecker, A.S. 1993. Biodiversity conservation in running waters. BioScience 43(1), 32-43.

Bell, S.S., Fonseca, M.S., Motten, L.B. 1997. Linking restoration and landscape ecology. Restoration Ecology 5(4), 318-323.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecological Monographs 27, 325-349.

Brown, K.S. Jr., 1991. Conservation of insects and their habitats: insects as indicators. In The conservation of insects and their habitats, eds. N.M. Collins and J.A. Thomas, pp. 350-404. Academic Press, London.

Brown, V.K., Southwood, T.R.E., 1983. Trophic diversity, niche breadth and generation times of exopterygote insects in a secondary succession. Oecologia 56, 220-225.

Buchwald, R., 1992. Vegetation and dragonfly fauna characteristics and examples of biocenological field studies. Vegetatio 101, 99-107.

Bulánková, E., 1997. Dragonflies (Odonata) as bioindicators of environmental quality. Biologia 52(2), 177-180.

Castella, E., 1987. Larval Odonata distribution as a describer of fluvial ecosystems: The Rhône and Ain Rivers, France. Advances in Odonatology 3, 23-40.

Chovanec, A., Waringer, J., 2001. Ecological integrity of river-floodplain systems – assessment by dragonfly surveys (Insecta: Odonata). Regulated Rivers Research and Management 17, 493-507.

Clark, T.E., 1991. Dragonflies as habitat indicators of the Sabie River in the Kruger National Park. MSc. Thesis. University of Natal, Pietermaritzburg.

Clark, T.E., Samways, M.J., 1996. Dragonflies (Odonata) as indicators of biotope quality in the Kruger National Park, South Africa. Journal of Applied Ecology 33, 1001-1012.

Clarke, K.R., Warwick, R.M., 2001a. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Marine Ecological Progress Series 216, 265-278.

Clarke, K.R., Warwick, R.M., 2001b. Change in marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd edn. PRIMER-E Ltd, Plymouth.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18, 117-143.

Connell, J. H., 1978. Diversity in tropical rainforests and coral reefs. *Science* 199, 1302-1310.

Corbet, P.S., 1999. Dragonflies: Behaviour and Ecology of Odonata. Harley Books, Colchester, United Kingdom.

Davies, B., Day, J., 1998. Vanishing Waters. University of Cape Town Press, Cape Town.

Davis, B.N.K., 1989. Habitat creation for butterflies at a landfill site. The Entomologist 108, 109-122.

Day, J.A., King, J.M., 1995. Geographical patterns, and their origins, in the dominance of major ions in South African rivers. South African Journal of Science 91, 299-306.

Department of Water Affairs and Forestry, 2003. The Environmental Impacts of Invading Alien Plants in South Africa. Working for Water, Cape Town.

Dempster, J.P., 1991. Fragmentation, isolation and the mobility of insect populations. In The Conservation of Insects and their Habitats, eds. N.M. Collins, J.A.Thomas, pp. 143-154. Academic Press, London.

Dickens, C.W.S., Graham, P.M., 2002. The South African Scoring System (SASS) version 5 rapid bioassessment system for rivers. African Journal of Aquatic Science 27, 1-10.

Donnelly, D., Giliomee, J.H., 1985. Community structure of epigaeic ants in a pine plantation and newly burnt fynbos. Journal of the entomological Society of southern Africa 48, 259-265.

Downes, P.W., Skinner, K.S., Kondolf, G.M., 2002. Rivers and streams. In Handbook of Ecological Restoration. Volume 2. Restoration in Practice, eds. M.R. Perrow, A.J. Davy, pp. 267-295. Cambridge University Press, Cambridge.

Dufrêne, M., Legendre, P., 1997. Species assemblages an indicator species: the need for a flexible assymetrical approach. Ecological Monographs 67(3), 345-366.

Gibbons, D.W., Pain, D., 1992. The influence of river flow rate on the breeding behaviour of *Calopteryx* damselflies. Journal of Animal Ecology 61, 283-289.

Haddad, N., 2000. Corridor length and patch colonization by a butterfly, *Junonia coenia.* Conservation Biology 14(3), 738-745.

Harrison, A.D., Agnew, J.D., 1962. The distribution of invertebrates endemic to acid streams in the Western and Southern Cape Province. Annals of the Cape Provincial Museums II, CSIR Reprint No. RW 121, Pretoria, South Africa.

Hawking, J.H., New, T.R., 2003. Interpreting dragonfly diversity to aid in conservation assessment: lessons from the Odonata assemblage at Middle Creek, north-eastern Victoria, Australia. Journal of Insect Conservation 6, 171-178.

Hellawell, J.M., 1991. Development of a rationale for monitoring. In Monitoring for Conservation and Ecology, ed. B. Goldsmith, pp. 3-14. Chapman and Hall, London.

Hill, B.T., Beinlich, B., Plachter, H., 1999. Habitat preferences of *Lestes barbarus* (Fabricius 1798) (Odonata Lestidae) on a low-intensity cattle pasture in the Sava floodplain (Croatia). Verhandelungen Gesellschaft fur Oekologie 29, 539-545.

Holmes, P.M., 1989. Decay rates in buried alien *Acacia* seed populations of different density. South African Journal of Botany 55(3), 299-303.

Holmes, P.M., Marais, C., 2000. Impacts of alien plant clearance on vegetation in the mountain catchments of the western Cape. South African Forestry Journal 189, 113-117.

Holmes, P.M., Richardson, D.M., van Wilgen, B.W., Gelderblom, C., 2000. Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration. Austral Ecology 25, 631-639.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54, 187-211.

Jenkins, D.W., 1971. Global biological monitoring. In Man's Impact on Terretrial and Oceanic Ecosystems, eds. W.H. Matthews, F.E. Smith, E.D. Goldberg, pp. 351-370. MIT, Cambridge, Massachusetts.

Johns, M., 1993. Are all trees green? Africa-Environment and Wildlife 1(3), 77-85.

Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F., Sanjayan, M.A., 1993. Terrestrial arthropod assemblages: their use in conservation planning. Conservation Biology 7, 796-808.

Kemper, N.P., 2001. RVI Riparian Vegetation Index. WRC Report No. 850/3/01. Water Research Commission, Pretoria.

Lawrence, J.M., Samways, M.J., 2002. Influence of hilltop vegetation type on an african butterfly assemblage and its conservation. Biodiversity and Conservation 11, 1163-1171.

King, J.M, Schael, D.M., 2001. Assessing the ecological relevance of a spatially-nested geomorphological hierarchy for river management. WRC Report No. 754/1/01. Water Research Commission, Pretoria.

Kinvig, R.G., Samways, M.J., 2000. Conserving dragonflies (Odonata) along streams running through commercial forestry. Odonatologica 29(3), 195-208.

Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.F., Sanjayan, M.A., 1993. Terrestrial arthropod assemblages: their use in conservation planning. Conservation Biology 7, 796-808.

Lombard, A.T., 1995. The problems with multi-species conservation: do hotspots, ideal reserves and existing reserves coincide? South African Journal of Zoology 30, 145-163.

Mac Arthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Manly, B.F.J., 1990. Randomization and Monte Carlo methods in biology. Chapman and Hall, London.

Maridet, L., Wasson, J-G., Philippe, M., Amoros, C., Naiman, R.J., 1998. Trophic structure of three streams with contrasting riparian vegetation and geomorphology. Archiv für Hydrobiologie 144, 61-85.

May, N.W., 1991. Thermal adaptations of dragonflies, revisited. Advances in Odonatology 5, 71-88.

McGeoch, M.A., 1998. The selection, testing and application of terrestrial insects as bioindicators. Biological Reviews 73, 181-201.

McGeoch, M.A., 2002. Bioindicators. In Encyclopaedia of Envirometrics, eds. A.H. El-Shaarawi, W.W. Piegorsch, pp. 186-189. John Wiley, Chichester.

McGeoch, M.A., Samways, M.J., 1991. Dragonflies and the thermal landscape: implications for their conservation (Anisoptera). Odonatologica 20(3), 303-320.

McGeoch, M.A., van Rensburg, B.J., Botes, A., 2002. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. Journal of Applied Ecology 39, 661-672.

McNeely, J.A., Gadgil, M., Leuèque, C., Padoch, C., Redford, K., 1995. Human influences on biodiversity. In Global Biodiversity Assessment, ed. V.H. Heywood, pp. 711-822. Cambridge University Press, Cambridge.

Moore, N.W., 1991. The development of dragonfly communities and the consequences of territorial behaviour: a 27-year study of small ponds at Woodwalton Fen, Cambridgeshire, United Kingdom. Odonatologica 20, 203-231.

Moore, N.M., 1997. Status Survey and Conservation Action Plan. Dragonflies. IUCN/SSC Odonata specialist group, IUCN, Gland and Cambridge.

Morely, S.A., Karr, J.R., 2002. Assessing and restoring the health of urban streams in the Puget Sound Basin. Conservation Biology 16(6), 1498-1509.

Muotke, T., Laasonen, P., 2002. Ecosystem recovery in restored headwater streams: the role of enhanced leaf retention. Journal of Applied Ecology 39, 145-156.

Myers, N., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853-858.

New, T.R., 1993. Effects of exotic species on Australian native species. In Perspectives on Insect Conservation, eds. K.J. Gaston, T.R. New, M.J. Samways, pp. 155-170. Intercept, Andover.

Noss, R.F., 1991. Landscape connectivity: different functions at different scales. In Landscape Linkages and Biodiversity, pp. 27-39. Island Press, Washington.

Oelofse, G.H.R., 1996. Distribution and ecological correlates of dragonflies (Odonata) in South Africa. MSc thesis, University of Cape Town, Cape Town.

Økland, R.H., 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? Journal of Vegetation Science 7, 289-292.

Ormerod, S.J., Weatherley, N.S., Merrett, 1990. The influence of conifer plantations on the distribution of the golden ringed dragonfly *Cordulegaster boltoni* (Odonata) in Upland Wales. Biological Conservation 53, 241-251.

Ormerod, S.J., Rundle, S.D., Clare, E., Duglas, A., 1993. The influence of riparian management on the habitat structure and macroinvertebrate communities of upland streams draining plantation forests. Journal of Applied Ecology 30, 13-24.

Osborn, R., 1995. Niche and life-history differences in five highly sympatric species of *Trithemis* dragonflies (Odonata: Libellulidae). MSc thesis, University of Natal, Pietermaritzburg.

Osborn, R., Samways, M.J., 1996. Determinants of adult dragonfly assemblage patterns at new ponds in South Africa. Odonatologica 25(1), 49-58.

Palmer, M.W., 1993. Putting the things in even better order: the advantages of canonical correspondence analysis. Ecology 74(8), 2215-2230.

Pienaar, E., Boucher, C., Brown, C., 2003. Distribution of *Acacia mearnsii* seed along depth and lateral profiles in natural and infested stands along selected rivers in the Breede River system. Unpublished report. Department of Botany, University of Stellenbosch, South Africa.

Pinhey, E.C.G., 1951. The dragonflies of South Africa. Transvaal Museum Memoir No. 5, 1-335.

Pinhey, E.C.G., 1978. Odonata. In Biogeography and Ecology of Southern Africa, ed. M.J.A. Werger, A.C. Bruggen, pp. 723-731. Junk, The Hague.

Pinhey, E.C.G., 1984. A survey of the dragonflies (Odonata) of South Africa. Part 1. Journal of the entomological Society of southern Africa 47, 147-188.

Pinhey, E.C.G., 1985. A survey of the dragonflies (Odonata) of South Africa. Part 2 Anisoptera. Journal of the entomological Society of southern Africa 48, 1-48.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C., Gibbons, D.W., 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. Nature 365, 335-337.

Purse, V.B., Hopkins, G.W., Day, K.J., Thompson, D.J., 2003. Dispersal characteristics and management of a rare damselfly. Journal of Applied Ecology 40, 716-728.

Richardson, D.M., van Wilgen, B.W., 2004. Invasive alien plants in South Africa: how well do we understand the ecological impacts? South African Journal of Science 100, 45-52.

Roque, F.O., Trivinho-Strixino, S., Strixino, G., Agostinho, R.C., Fogo, J.C., 2003. Benthic macroinvertebrates in streams of the Jaragua State Park (Southeast of Brazil) considering multiple spatial scales. Journal of Insect Conservation 7, 63-72.

Rosenberg, D.K., Noon, B.R., Meslow, E.C., 1997. Biological corridors: form, function and efficacy. BioScience 47(10), 677-687.

Rutt, G.P., Weatherley, N.S., Ormerod, S.J., 1989. Microhabitat availability in Welsh moorland and forest streams as a determinant of macroinvertebrate distribution. Freshwater Biology 22, 247-261.

Samways, M.J., 1989. Insect conservation and the disturbance landscape. Agriculture, Ecosystems and the Environment 27, 183-194.

Samways, M.J., 1992. Dragonfly conservation in South Africa: a biogeographical perspective. Odonatologica 21, 165-180.

Samways, M.J., 1993a. A spatial and process sub-regional framework for insect and biodiversity conservation research and management. In Perspectives on Insect Conservation, eds. K.J. Gaston, T.R. New, M.J. Samways, pp. 1-28. Intercept, Andover.

Samways, M.J., 1993b. Dragonflies (Odonata) in taxic overlays and biodiversity conservation. In Perspectives on Insect Conservation, eds. K.J. Gaston, T.R. New, M.J. Samways, pp. 111-124. Intercept, Andover.

Samways, M.J., 1994. Insect Conservation Biology. Chapman and Hall, London.

Samways, M.J., 2002. Red listed Odonata species of Africa. Odonatologica 31, 117-128.

Samways, M.J., 2003. Threats to the tropical island dragonfly fauna (Odonata) of Mayotte, Comoro archipelago. Biodiversity and Conservation 12, 1785-1792.

Samways, M.J., 2005. National Red List of South African dragonflies (Odonata). Odonatologica (in press).

Samways, M.J., Caldwell, P., 1989. Flight behaviour and mass feeding swarms of *Pantala flavescence* (Fabricius) (Odonata: Anisoptera: Libellulidae). Journal of the entomological Society of southern Africa 52, 326-328.

Samways, M.J., Caldwell, P.M., Osborn, R., 1996. Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. Agriculture, Ecosystems and Environment 59, 19-32.

Samways, M.J., Moore, S.D., 1991. Influence of exotic conifer patches on grasshopper (Orthoptera) assemblages in a grassland matrix at a recreational resort, Natal, South Africa. Biological Conservation 57, 117-157.

Samways, M.J., Steytler, N.S., 1996. Dragonfly (Odonata) distribution patterns in urban and forest landscapes, and recommendations for riparian management. Biological Conservation 78, 279-288.

Samways, M.J., Taylor, S., 2004. Impacts of invasive alien plants on Red-Listed South African dragonflies (Odonata). South African Journal of Science 100, 78-80.

Samways, M.J., Taylor, S., Tarboton., W., 2005. Extinction reprieve following alien removal. Conservation Biology 19, 1329-1330.

Saunders, J.J., Meeuwig, J.J., Vincent, A.C.J., 2002. Freshwater protected areas: strategies for conservation. Conservation Biology 16(1), 30-41.

Schmidt, E., 1985. Habitat inventariszation, characterization and bioindication by a "representative spectrum of Odonata species". Odonatologica 14(2), 127-133.

Siegfried, W.R., Brown, C.A., 1992. The distribution and protection of mammals endemic to Southern Africa. South African Journal of Wildlife Research 22(1), 11-16.

Simberloff, D.S. 1998. Flagships, umbrellas, and keystones: is single-species management passe in the landscape era? Biological Conservation 83, 247-257.

Sternberg, K., 1994. Niche specialisation in dragonflies. Advances in Odonatology 6, 177-198.

Stewart, D.A.B., Samways, M.J., 1998 Conserving dragonfly (Odonata) assemblages relative to river dynamics in an African savanna game reserve. Conservation Biology 12(3), 683-692.

Steytler, N.S., 1994. Dragonfly distribution patterns relative to urban and forest landscapes. MSc. thesis. University of Natal, Pietermaritzburg.

Steytler, N.S., Samways, M.J., 1995. Biotope selection by adult male dragonflies (Odonata) at an artificial lake created for insect conservation in South Africa. Biological Conservation 72, 381-386.

Stork, N.E., Samways, M.J., 1995. Inventorying and monitoring of biodiversity. In Global Biodiversity Assessment, ed. V.H. Heywood, pp. 453-544. Cambridge University Press, Cambridge.

Stubbs, A., Warren, P., 1991. Aquatic water margin habitats; ecological principles and problems. In Habitat Conservation for Insects – a Neglected Green Issues, eds. R. Fry, D. Lonsdale, pp. 151-158. The Amateur Entomologist 21. The Amateur Entomologists' Society, Essex.

Tarboton, W., Tarboton, M., 2002. A fieldguide to the dragonflies of South Africa. W&M Tarboton, Modimolle, South Africa.

Ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67, 1167-1179.

Ter Braak, C.F.J., 1988. Chapter 5. Ordination. In Data Analysis in Community Ecology, ed. R.H.G. Jongman, C.J.F. ter Braak, O.F.R. van Tongeren, pp. 91-173. Cambridge University Press, Cambridge.

Ter Braak, C.F.J., 1992. Permutation versus bootstrap significance tests in multiple regression and ANOVA. In Bootstrapping and related techniques, ed. K.H. Jökel, G. Rothe, W. Sendler, pp. 79-86. Springer Verlag, Berlin.

Ter Braak, C.J.F., Smilauer, P., 2002. CANOCO reference manual and user's guide to Canoco for Windows: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, New York.

Ter Braak, C.J.F., Verdonschot, P.F.M., 1995. Canonical correspondence analysis and related methods in aquatic ecology. Aquatic Sciences 57(3), 153-185.

Underwood, A.J., 1998. Experiments in Ecology. Cambridge University Press, Cambridge.

Usher, M.B., 1988. Biological invasions of nature reserves: a search for generalizations. Biological Conservation 44, 119-135.

Usher, M.B., Jefferson, R.G., 1993. Creating new and successional habitats for arthropods. In The Conservation of Insects and their Habitats, eds. N.M. Collins, J.A.Thomas, pp. 263-293. Academic Press, London.

Usher, M.B., Smart, L.M., 1988. Recolonization of burnt and cut heathland in the New York Moors by Arachnids. Naturalist 113, 103-111.

Vane-Wright, R.I., 1993. Systematics and the conservation of biodiversity: global, national and local perspectives. In Perspectives on Insect Conservation, eds. K.J. Gaston, T.R. New, M.J. Samways, pp. 197-212. Intercept, Andover.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Science 37, 130-137.

Van Rensburg, B.J., McGeoch, M.A., Chown, S.L., Van Jaarsveld, A.S., 1999. Conservation of heterogeneity among dung beetles in the Maputoland Centre of Endemism, South Africa. Biological Conservation 88, 145-153.

Vegter, J.R., 1995. Geology map of South Africa with simplified lithostratigraphy for geohydrological use. Water Research Commission TT 74/95, Pretoria, South Africa.

Verdonschot, P.F.M., ter Braak, C.J.F., 1994. An experimental manipulation of oligochaete communities in mesocosms treated with chlorpyrifos or nutrient additions: multivariate analysis with Monte Carlo permutation tests. Hydrobiologia 278, 251-266.

Walker, B.M., Steffen, W.L., 1999. Interactive and integrated effects of global change on terrestrial ecosystems. In The Terrestrial Biosphere and Global Change: Implications for Natural and Managed Ecosystems, eds. B. Walker, W.L. Steffen, J. Canadell, J. Ingram, pp 329-375. International Geosphere Program Book Series 4, Cambridge University Press, Cambridge.

Ward, J.V., Stanford, J.A., 1983. The intermediate disturbance hypothesis: an explanation for biotic diversity patterns in lotic ecosystems. In Dynamics of Lotic Ecosystems, eds. T.D. Fontaine, S.M. Bartell, pp. 247-356. Ann Arbor Press, Ann Arbor, Michigan.

Warren, C.E., 1971, Biology and Water Pollution Control. W.B. Saunders Co., Philadelphia.

Wiens, J.A., 1995. Habitat fragmentation: island vs. landscape perspectives on bird conservation. Ibis 137, 97-104.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. BioScience 48, 607-615.

Wildermuth, H., Spinner, W., 1991. Visual cues in oviposition site selection by *Somatochlora arctica* (Zetterstedt) (Anisoptera: Corduliidae). Odonatologica 20, 357-367.

Williams, K.S., 1997. Terrestrial arthropods as ecological indicators of habitat restoration in southwestern North America. In Restoration Ecology and Sustainable Development, eds. K.M. Urbanska, N.R. Webb, P.J. Edwards, pp. 238-258. Cambridge University Press, Cambridge.

Willson, J.D., Dorcas, M.E., 2003. Effects of habitat disturbance on stream salamanders: implications for buffer zones and watershed management. Conservation Biology 17(3), 763-771.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperilled species in the United States. BioScience 48, 607-615.

Wilson, D.S., Yoshimura, J., 1994 On the coexistence of specialists and generalists. The American Naturalist 144, 692-707.

Wood, P.A., Samways, M.J., 1991. Landscape element pattern and continuity of butterfly flight paths in an ecologically landscaped botanic garden, Natal, South Africa. Biological Conservation 58, 149-166.

WRI/IUCN/UNEP, 1992. Global Biodiversity Strategy: Guidelines for Action to Save, Study and Use Earth's Biotic Wealth Sustainably and Equitably. WRI/IUCN/UNEP, World Resources Institute, Washington DC.

Zavaleta, E.S., Hobbs, R.J., Mooney, H.A., 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology and Evolution 16(8), 454-459.

Zwick, P., 1992. Stream habitat fragmentation – a threat to biodiversity. Biodiversity and Conservation 1, 80-97.

Chapter 3
Response of benthic macroinvertebrate assemblages to the removal of invasive alien trees in the Western Cape

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Abstract

Invasive alien trees, especially *Acacia* species, are a great threat to biodiversity in South African rivers. The national Working for Water Programme is addressing the alien problem by removing alien trees from river margins. The concern is that this may be creating even further disturbance by affecting water quality and habitats. In particular, how is this affecting rare and endemic species? Benthic macroinvertebrates were assessed along two Western Cape rivers in alien-invaded, cleared and natural sites between December and March. SASS5, a qualitative, rapid bioassessment technique, based on the sensitivity of the families present, was used as a measure of river health and, indirectly, of water quality. SASS indicated a decline in water quality conditions after alien clearing, a likely response to the greater insolation and apparent erosion of cleared banks, resulting in elevated temperatures and suspended solids and lowered oxygen levels. Sensitive, endemic taxa were lost after clearing, being replaced by more tolerant, widespread taxa. Community responses to alien disturbance and other environmental factors were analysed using PRIMER and CANOCO software. Analyses were conducted at morphospecies and family level to determine the most useful level of taxonomic resolution. Between-river and seasonal effects dominated assemblage patterns, so that generalisations were difficult. However, cleared and natural sites were more similar to each other than to alien sites, suggesting some measure of post-clearing recovery, particularly along the Molenaars River. Abundance and richness were also not found to differ significantly in natural and cleared sites. Vegetation types, oxygen and width were important environmental variables affecting distribution patterns. Recovery of invertebrate biodiversity appears to follow the recovery of indigenous vegetation, with endemic, sensitive taxa only recovering after the recovery of indigenous fynbos. Therefore, for biodiversity objectives to be achieved, it is essential that indigenous plants are maintained and cultivated during and after clearing to encourage the recovery of endemic and sensitive taxa. The Indicator Value method revealed Heptageniidae and Teloganodidae to be potential detectors of alien invasion and recovery after clearing. Therefore, where SASS detects overall changes in river health, without identifying the cause, detector families may link these changes to alien disturbance, thus proving useful in long-term assessments and monitoring. Teloganodidae, being sensitive and endemic, may additionally be useful for identifying biodiverse areas for protection or prioritising areas for clearing. To achieve biodiversity goals, it is

recommended that alien clearing programmes change the emphasis from clearing to restoration, assessment and protection. A number of recommendations are made in this regard.

Keywords: Benthic macroinvertebrates, Alien trees; Alien removal; Rehabilitation; Rivers; Biodiversity; Ecological monitoring; Riparian vegetation; Western Cape; South Africa.

1. Introduction

Alien invasion impacts directly on biodiversity by out-competing indigenous species and reducing structural diversity of the vegetation (Richardson and van Wilgen, 2004). This results, either directly or indirectly, in the demise of rare species and the displacement of indigenous species (New, 1993), thus decreasing biodiversity. Ultimately, this affects the structure and function of the ecosystem and its associated ecosystem services (Usher, 1988). The Western Cape has a unique and highly endemic freshwater fauna, many of which remain undescribed or undetected (Wishart *et al.*, 2003). Considered to be descendants of temperate Gondwanan fauna (Harrison, 1965), 64% of freshwater invertebrates in the Cape Floristic Region are considered endemic (Wishart and Day, 2001). These too may be affected by alien invasion, with obvious implications for management of freshwater systems.

Dense stands of invasive trees along river margins cause changes in habitat structure, fire regimes, hydrology and water quality. Water quality changes may involve changes in light regime, temperature and oxygen (as a result of shading by alien trees), changes in the patterns of allochthonous input of leaf litter, changes in nutrient cycling, pH and turbidity and increased erosion and sedimentation (Rutt *et al.*, 1989; Davies and Day, 1998; Maridet *et al.*, 1998). Alien trees, especially *Acacia mearnsii* De Willd. and *A. longifolia* (Andr.) Willd., have dense canopies that shade out habitats and prevent the growth of understorey plants such as sedges, reeds and grasses (Kinvig and Samways, 2000; Samways *et al.*, 1996), thus altering the availability and quality of marginal habitats. Marginal vegetation may be used by benthic larvae for nursery areas,

food or protection and by adults for perch or oviposition sites. Alien riparian vegetation therefore affects both water quality and riparian and aquatic habitats.

The systematic removal of alien vegetation is being conducted by the national Working for Water Programme and is expected to considerably increase the long-term survival of rare and endemic species. Riverine trees, such as *Acacia* species, are initially cleared by felling and burning, while follow-up treatments use herbicides and burning to prevent resprouting. This, in itself, is a further disturbance to the river system as it may once again cause major changes to water quality and instream and riparian habitats. Removal of riparian vegetation reduces the amount of organic inputs via leaf litter, branches or twigs, as well as fine particulate organic matter and dissolved organic matter (Bunn *et al.*, 1999). There is also a dramatic reduction in shade, resulting in increasing water temperatures, which reduce the solubility of oxygen. Temperatures will also fluctuate more widely after alien removal (Allan and Flecker, 1993). Greater exposure to sunlight results in the growth of macrophytes and filamentous algae, which are less palatable to herbivores (Bunn *et al.*, 1999). Removal of riparian vegetation also leads to increased runoff from catchments, resulting in increased salinity and nutrient loading. Bank stability is decreased, resulting in increased erosion and increased sediment and suspended solid loads, accompanied by increased turbidity. In addition to water quality changes, there may be a loss of instream habitat or a decline in habitat quality as a result of changes in flow regime, substrate modification or vegetational changes (Vuori and Joensuu, 1996).

It is likely, therefore, that alien clearing will affect, either directly or indirectly, benthic macroinvertebrate communities. No previous research has been done to determine the effects of alien disturbance on aquatic communities in the Western Cape. Successful removal of invasive alien plants along rivers and the subsequent rehabilitation of indigenous vegetation could result in increased biological diversity. However, to achieve biodiversity objectives, it is imperative that the process does not cause the loss of endemic or rare species that are of conservation importance.

This study aims to assess, not only the effects of alien invasion along riparian corridors, but also the effectiveness of the Working for Water Programme in terms of biodiversity conservation of benthic macroinvertebrates. An attempt will be made to determine the requirements for rehabilitation of cleared river margins and to make recommendations on how Working for Water can manage the process according to biodiversity criteria. In addition, an attempt will be made to identify potential indicators or detectors that could be used to monitor the recovery or deterioration of sites.

1.1. Benthic macroinvertebrates as bioindicators

In aquatic systems, benthic macroinvertebrates have widely been used as bioindicators, primarily because of the sensitivity of several taxa to impairment of water quality. They are also diverse and ubiquitous and are therefore affected by a wide range of disturbances in a wide range of habitats (Johnson *et al.*, 1993). In their aquatic phase, they are relatively sedentary and therefore represent the location being sampled, thus allowing for the analysis of spatial patterns of disturbance. They are also easily sampled and relatively abundant.

Numerous bioassessment techniques that use benthic macroinvertebrates as indicators have been developed in the past few decades, varying in complexity and ease of implementation (e.g. Chessman, 1995; Chutter, 1972, 1998; Wright *et al.*, 1984). These methods are reviewed in Rosenberg and Resh (1993). Three basic types of indices exist: diversity, comparison (similarity or dissimilarity) and biotic (Resh and Jackson, 1993). Biotic indices have been widely applied to stream ecosystems (Johnson *et al.*, 1993) and, in many countries, are the primary measure of ecosystem health (Gerritsen *et al.*, 2000). They are used to infer the ecological health of a river while also providing an indirect measure of water quality (Rutherfurd *et al.*, 2000a). Disturbance effects that have been detected using biotic indices include sewage (e.g. Chessman, 1994; Wright *et al.*, 1995), wastewater discharges (Dickens and Graham, 1998), trout farm effluent (Brown,

1997), organic pollution (Cao *et al.*, 1997), agriculture and afforestation (Quinn *et al.*, 1997), metal pollution (Carlisle and Clements, 1999) and insecticides (Wallace *et al.*, 1996). Biotic indices therefore have applications in conservation, pollution control and biological monitoring and river management.

While quantitative indices are more informative and comprehensive, time and financial limitations have led to a proliferation of qualitative rapid assessment biotic indices, such as the BMWP system (Biological Monitoring Working Party, e.g. Wright, 1995) and the Australian SIGNAL biotic index (Stream Invertebrate Grade Number Average Level, Chessman, 1995). In South Africa, the South African Scoring System (SASS) (Chutter, 1998) is routinely used in the rapid assessment of water quality and river health. A 'healthy' river can be regarded as one that supports a biologically diverse, indigenous community that includes aquatic species that are sensitive to disturbance events (Rutherfurd *et al.*, 2000a).

SASS is a qualitative technique that involves sampling the aquatic macroinvertebrates on the streambed and in the marginal vegetation. A score is assigned to each family present, based on the known sensitivity/tolerance of that family to deterioration in water quality (Dallas, 1995). The total of these SASS scores provides an index of river health, although the average score per taxon (ASPT) is often regarded as a more robust measure. SASS has been tested and evaluated by Brown (2001) and Dallas (1995, 1997, 2000).

SASS is fast and cost-effective and has been incorporated into routine assessments performed by the National River Health Programme (Uys *et al.*, 1996). The National River Health Programme is a national programme aimed at assessing the ecological health and overall integrity of aquatic ecosystems in South Africa (Roux, 1997), making use of a range of bioindicators (e.g. fish, invertebrates, vegetation and habitat). The results also inform State of Rivers reports.

SASS is also becoming increasingly important since the enactment of the National Water Act (No. 36 of 1998). This act recognises that "the protection of the quality of water resources is necessary to ensure sustainability of the nation's water resources" and that there is a "need for the integrated management of all aspects of water resources". It makes provision for a national water resource strategy which includes the development of a classification system for water resources and the determination of resource quality objectives. These objectives may relate to, amongst others, "the characteristics and quality of the water resource...and the characteristics and distribution of aquatic biota". The Act also makes provision for the determination of a national reserve which is the quality and quantity of water required to "satisfy human needs" and to "protect aquatic ecosystems...to secure ecologically sustainable development and use". All these components are concerned with resource quality which is defined by the act as the quality of all aspects of water resources including (amongst others) "the character and condition of the instream and riparian habitat and the characteristics, condition and distribution of the aquatic biota". Clearly, bioassessment will play a pivotal role in the classification of rivers, the determination of resource quality objectives and the determination of the ecological reserve.

Invertebrate taxa that contribute substantially to SASS scores, in terms of their sensitivity, include the Ephemeroptera, Plecoptera, Trichoptera and Odonata (Dickens and Graham, 2002). These taxa are the most commonly used taxa in bioassessment. The Ephemeroptera, Plecoptera and Trichoptera are often collectively referred to as the EPT taxa (Resh and Jackson, 1993) and EPT taxa richness is widely used in North America as a measure of physical and chemical conditions of river water (e.g. Lenat and Crawford, 1994). The majority of taxa within these orders are pollution-sensitive and species richness of the EPT taxa is often used as an index of water quality (Lenat, 1988; Resh and Jackson, 1993). The Odonata have the added advantage of being relatively large, easily sampled and identified to family level and have been used as indicator species in several studies (e.g. Bulánková, 1997; Clark and Samways, 1996; Sahlén and

Ekestubbe, 2001; Schmidt 1985; Stewart and Samways, 1998). The EPT and Odonata (EPT+O) spend their larval or nymphal stages on the streambed but have winged adults.

The distribution and abundance of benthic macroinvertebrates can be affected by factors other than water quality, such as current velocity or nature of the substratum (Rosenberg and Resh, 1993). Moreover, different taxa may respond differently to a particular disturbance. Therefore, quantitative multivariate assessment, used in addition to SASS, can provide more specific information on community responses.

However, multivariate ecological analyses usually require identifications to species level (Resh and McElravy, 1993) and these are often fraught with taxonomic difficulties and inconsistencies, making this a time-consuming and unreliable assessment tool. Juveniles, in particular, are difficult to identify. Family-level identification, on the other hand, is more feasible and therefore more valuable for comparisons because it is achievable in all studies (Bournaud *et al.*, 1996). It has been argued that family-level identifications are more useful than species-level identifications for impact assessments because, at this higher taxonomic level, the natural environmental 'noise' does not mask the community response (Warwick, 1993; Brown, 2001). On the other hand, it has been noted that the different sensitivities of species within a family may make species-level indicators more useful (e.g. amongst Trichoptera - de Moor and Scott, 2003) (Guerold, 2000). Therefore, the additional question is asked: what ecological value can be assigned to family-level analyses and what information can be shown at what scale?

2. Methods

2.1. Study Area

The Western Cape is home to the Cape Floristic Region, an internationally recognised biodiversity hotspot (Myers *et al.*, 2000). The aquatic invertebrates of this region exhibit a high

degree of endemism, a combined product of climatic, geological, geomorphological and vegetation characteristics (Harrison and Agnew, 1962). Vegetation typically found in the upper catchments comprises sclerophyllous fynbos. The region has a mediterranean climate with hot, dry summers and cool, rainy winters. Water flowing over the quartzitic sandstone of the mountains, which form part of the Table Mountain Group (Vegter, 1995), is characteristically acidic and low in nutrients and dissolved solids, the latter consisting predominantly of sodium and chloride (Day and King, 1995).

Study sites were located along the Molenaars and Rondegat Rivers (Fig. 1), both of which had had alien vegetation removed from sections of their riparian zones over the past two years. While the Rondegat River forms part of the Olifants River catchment, the Molenaars River forms part of the Breede River catchment. Along each river, three disturbance regimes were identified: natural (indigenous riparian vegetation), alien (invasive alien trees, generally *Acacia mearnsii*) and cleared (alien trees removed). Five sites were selected from each disturbance regime along each river (i.e. 15 sites per river). Sites were 15 m long and were spaced at intervals of about 20 m. Sampling was conducted during January and March, generating a total of 20 alien, 22 cleared and 20 natural samples. To remove the effects of zonation, all sites were located in the foothill zone.

Samples were also taken from the Dwars, Witte and Holsloot Rivers, all within the Breede River catchment (Fig. 1). However, only one sample was collected from each disturbance regime in each of these rivers, generating nine samples in total.

Alien sites varied considerably in terms of tree density and, therefore, in factors such as shade, bank exposure and the presence of marginal vegetation. Three alien sites along the Molenaars River had dense stands of *A. mearnsii* with over 70% canopy cover and shade. Alien trees were generally *A. mearnsii* and, to a lesser extent, *A. longifolia*, although *Eucalyptus camaldulensis* Dehnh. occurred amongst the *Acacia* along the Rondegat River.

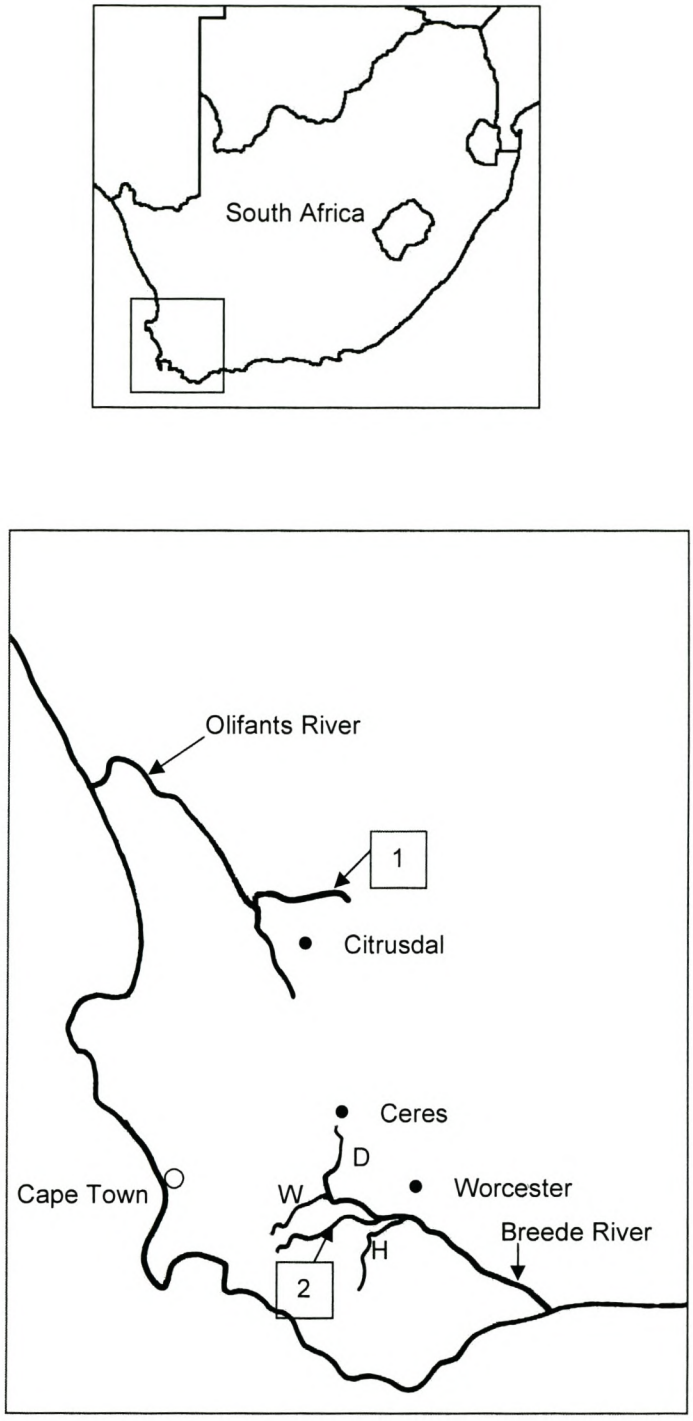


Fig. 1. Location of the two Western Cape rivers studied. 1 = Rondegat River, 2 = Molenaars River. Additional samples were taken from the Dwars River (D), the Witte River (W) and the Holsloot River (H).

Cleared sites also varied in terms of the extent of recovery. Vegetation along the Molenaars River cleared sites had a high proportion of palmiet reed, *Prionium serratum* L.f. ('*Prionium*') and short indigenous trees and bushes, while sedge was more prevalent in Rondegat cleared sites. There was also extensive regrowth of *E. camaldulensis* saplings along the Rondegat River cleared sites.

Most natural sites had riparian thicket (consisting mostly of *Brabejum stellatifolium* L. and *Metrosideros angustifolia* [L.] Smith). For the sake of clarity, these were referred to as 'tall indigenous trees' to separate them from shorter indigenous bushes. Shading by these trees limited understorey growth of *Prionium* and grass, although a recent fire in natural sites along the Rondegat River resulted in an increase in *Prionium* and short fynbos elements.

2.2. Sampling methods

The benthic invertebrates were sampled at each site along the Rondegat and Molenaars Rivers, using the standardised SASS5 method of sampling (Dickens and Graham, 2002). Ten replicates were collected from each site, five during January and five during March. All available SASS biotopes was sampled: stones-in-current and stones-out-of-current (sampled collectively), marginal and aquatic vegetation (sampled collectively), gravel, sand and mud (sampled collectively) and handpicking or visual observation. Stones were kicked for between 2 and 5 minutes, while a kick net (300 x 300 mm frame, 950 μm mesh) was held immediately downstream of the sampled area. Vegetation was sampled by sweeping for a total of two meters through the vegetation below the water level. Loose substratum was agitated for 30 seconds. The dislodged animals collected in the net were tipped into a sorting tray where they were identified to family level. The SASS score was then calculated according to the families present. Because accuracy depends on the amount of debris collected as well as the experience of the sorter, for the purposes of this study, there was no standardised time limit for identifying animals, thus generating SASS scores that were based on a consistent level of accuracy. Ephemeroptera, Plecoptera, Trichoptera and Odonata were then

collected, preserved in 80% alcohol and later sorted to morphospecies with the help of identification guides (Barber-James and Lugo-Oritz, 2003; de Moor and Scott, 2003; Samways and Wilmot, 2003; Stevens and Picker, 2003). Individuals of each family and morphospecies were counted.

The habitats sampled were assessed using IHAS (Integrated Habitat Assessment System, McMillan, 1998) in conjunction with the SASS sample. IHAS takes into account, for example, stream width and depth, riparian vegetation and the presence of algae or disturbance, together with sampling effort and the proportion of each biotope sampled (i.e. stones, vegetation and substratum) (McMillan, 1998). When IHAS is related back to SASS, it indicates whether SASS scores truly reflected water quality, or merely the habitats that were sampled.

Riparian vegetation was classified into broad categories. These were: sedge/grass, alien *Acacia* spp., *Prionium* and indigenous trees and bushes (mostly *M. angustifolia* and *B. stellatifolium* but also including ericoid and proteoid fynbos shrubs, such as *Erica caffra* L. and *Brachylaena neriifolia* [L.f.] R. Br).

At each site, the following environmental variables were measured:

- river system (in order of increasing latitude: 1 = Rondegat, 2 = Molenaars. The rivers were less than 17' apart within the 19° longitude.)
- disturbance regime (1 = natural, 2 = cleared, 3 = alien)
- dissolved oxygen, temperature, pH and electrical conductivity (YSI 556MPS)
- flow (time taken for a floating object to be carried five metres)
- mean width and depth of river
- percentage of cobbles, gravel and sand in the river substrate
- percentage cover of each vegetation category given above (in a 2 m marginal recording zone)

- percentage cover of exposed soil on the banks (in a 1 m marginal recording zone)
- percentage canopy cover (percentage of river covered by trees)
- Coarse Particulate Organic Matter (CPOM) (scored between one and five according to the amount of debris collected in the SASS sample)
- total suspended solids (TSS) (River water was collected from high-flow areas and filtered through preweighed 45µm GF/F filters within 24 hours of sampling. The filters were oven-dried at 40°C for 24 hours, reweighed and the difference calculated.)
- percentage of the water surface with riffles (broken flow) and pools (no visible flow)

2.3. Data analyses

Data analysis was divided into two sections: (1) qualitative water quality assessment using SASS and (2) quantitative and multivariate analysis to determine community responses. The latter was performed at three levels of taxonomic complexity: family, morphospecies and presence/absence. Presence/absence analysis was performed on all benthic macroinvertebrate families collected in the SASS samples, while family and morphospecies abundances were performed on Ephemeroptera, Plecoptera, Trichoptera and Odonata only.

2.3.1. SASS

SASS, ASPT and IHAS scores were compared between cleared, alien and natural sites. Rivers and sampling month (i.e. season) were also compared. Analysis of variance and student's *t*-test were used to analyse for differences between means. The results were considered significant at $p < 0.05$. Because SASS does not conform to all the assumptions of normality, the Kruskal-Wallis test was used to confirm t-test significant differences. The differences were found to be consistent and only t-test results are presented.

The incidence and SASS scores of individual families were compared between disturbance regimes and discussed in terms of sensitivity to disturbance.

2.3.2. Quantitative analysis

Mean abundance and richness were calculated for alien, cleared and natural sites in both rivers. Analysis of variance and student's *t*-test were used to analyse for differences between means. Multivariate community analysis of abundance data was done using PRIMER v5.0 software (Clarke and Warwick, 2001). Sampling units with similar assemblage patterns were identified and grouped together in habitat clusters. This was achieved with the CLUSTER programme within the PRIMER software package. Hierarchical agglomerative clustering was performed on Bray-Curtis similarity matrices, using group-average linking, to produce dendrograms (Bray and Curtis, 1957). The data were fourth-root transformed to remove heterogeneity of variance (Underwood, 1998). Non-metric multi-dimensional scaling (MDS) visually displayed the relationships between the sampling units in the ordination analysis.

Analysis of similarity (ANOSIM – Clarke, 1993) was used to establish the significance of differences between sampling units and habitat clusters. ANOSIM is a non-parametric permutation procedure applied to the similarity matrix that underlies the ordination (Clarke and Warwick, 2001). This method overcomes the problem of non-normal probability distributions resulting from the dominance of zero values in multispecies abundance data, which prevent the assumptions of parametric multivariate analysis of variance (MANOVA) from being satisfied (Clarke and Warwick, 2001).

The family or morphospecies assemblages responsible for distinguishing habitat clusters were identified with the SIMPER (similarity percentages) routine. This examines the overall percentage contribution each taxon makes to the average dissimilarity between habitat clusters. SIMPER also

gives the assemblages that contribute most to within-group similarities, these taxa therefore being characteristic of that habitat cluster.

Indicator and detector families or morphospecies were identified for each habitat cluster using the indicator value (*IndVal*) method (Dufrêne and Legendre, 1997). The *IndVal* method combines the specificity of a taxon (uniqueness to a particular habitat type) and its fidelity (frequency within that habitat type) (Dufrêne and Legendre, 1997). Taxa with both a high specificity and fidelity to a habitat type will have a high indicator value (*IndVal* - expressed as a percentage).

IndVal is calculated as follows:

Specificity $A_{ij} = Nindividuals_{ij}/Nindividuals_{i}$

where $Nindividuals_{ij}$ is the mean number of taxon i across sites of group j, and $Nindividuals_{i}$ is the sum of the mean numbers of individuals of taxon i over all groups.

Fidelity $B_{ij} = Nsites_{ij}/Nsites_{j}$

where $Nsites_{ij}$ is the number of sites in cluster (habitat) j where taxon i is present, and $Nsites_{j}$ is the total number of sites in that cluster.

The percentage indicator value for taxon i in cluster j is:

$IndVal_{ij} = A_{ij} x\ B_{ij} x\ 100$

The *IndVals* were calculated for each family and morphospecies. Dufrêne and Legendre's (1997) random reallocation procedure was used to test the significance of the *IndVal* measure for each taxon. Taxa with significant *IndVals* of greater than say 70% (subjective choice, van Rensburg *et al.*, 1999) were regarded as characteristic indicator taxa for that habitat. Taxa with medium-range *IndVal* values (e.g. 50-70%) were regarded as detectors.

The environmental variables that were important in determining faunal composition were determined with Canonical Correspondence Analysis (CCA) (ter Braak, 1986) using CANOCO version 4.5 software (ter Braak and Smilauer, 2002). This is a direct gradient analysis technique that uses multiple regression to select linear combinations of environmental variables that account for most of the variation in the species scores on each axis. (In this study, family and morphospecies replaced species as the taxonomic unit). Therefore, the ordination diagram expresses the pattern of variation in the species data, together with the main relations between the species and each environmental variable (ter Braak, 1988). The method is considered to be fairly robust, accommodating, *inter alia*, skewed species distributions, interrelated environmental variables and incomplete environmental measurements (Palmer, 1993).

CCA ordination diagrams were used to display the distribution patterns underlying taxa or sites (points) as explained by the environmental variables (arrows). These diagrams are interpreted as follows: each environmental variable is represented by an arrow, which indicates its direction of maximum variation; dropping a perpendicular from a site or species point to the arrow shows the relative position of the site or species along the environmental gradient (represented by the arrow). This provides a means of visualising the differential habitat preferences of the species (ter Braak and Verdonschot, 1995). The length of the arrow is a measure of how much the species relative abundances differ along that environmental gradient (i.e. the rate of change of the weighted averages). The longer arrows are therefore more important in determining species distributions. The relative magnitudes of the canonical coefficients also indicate the relative importance of each environmental variable in predicting assemblage composition.

Included as nominal variables in the CCA were 'disturbance regime' and 'river system'. For the ordination diagrams, each disturbance class (i.e. natural, cleared, alien) was converted to a dummy variable (with a value of one if present in a sample, and zero if absent) and represented as a centroid (the average scores of the samples belonging to that class).

In addition to the overall CCA, a partial ordination was performed to eliminate between-river and seasonal effects. This was achieved by specifying 'river' and 'month' as co-variables. Partial ordination yields an ordination diagram of the residual variation in the species data after the covariable is factored out by multiple linnear regression (Verdonschot and ter Braak, 1994).

Forward selection was used to rank environmental variables in order of importance according to the eigenvalues produced (i.e. variation in the species data accounted for by that variable) if each variable was considered individually. Monte Carlo permutation tests (Manly, 1990; ter Braak, 1992), using 199 unrestricted random permutations, were performed to test the significance of the environmental variables on faunal distribution patterns. Environmental variables were first selected by forward selection and each tested individually as the only variable (marginal effects). Variables were then tested collectively with the addition of one variable at a time (conditional effects). The Monte Carlo permutation tests replace the *F*- and *t*-tests in forward selection in multiple regression.

3. Results

3.1. SASS

Although natural sites had the highest SASS scores, there was, on average, no overall significant difference between natural, cleared and alien disturbance regimes ($F = 2.44$, $P = 0.1$) (Table 1A). Overall ASPT scores were highest in alien sites but, again, there was no significant difference between disturbance regimes ($F = 2.66$, $P = 0.08$) (Table 1B). Only the Rondegat River showed a significant difference between disturbance regimes, with natural site scores being significantly higher than cleared or natural site scores. In contrast, Molenaars River SASS and ASPT scores were highest in alien sites, although not significantly so, while natural and cleared sites gave similar scores. Both SASS and ASPT scores differed significantly between rivers (Tables 1A and 1B), with the Molenaars River giving higher mean scores.

SASS scores did not, however, reflect the habitat sampled as measured by IHAS (Table 1C). IHAS scores were consistently lowest in alien sites and highest in natural sites, but did not differ significantly between rivers. SASS scores were therefore assumed to be a measure of water quality, and not a reflection of the habitat sampled.

A survey of three other Western Cape rivers (the Dwars, Witte and Holsloot Rivers) confirmed these findings with a significant difference between rivers ($F = 10.64$, $P = 0.01$) but not between disturbance regimes ($F = 0.49$, $P = 0.63$) (Table 2). Mean SASS scores tended to be highest in natural sites and lowest in alien sites, but this was not consistent across rivers. For example, in the Holsloot and Rondegat Rivers, alien scores were not much different to cleared scores, while, in the Molenaars River, natural scores were not much higher than cleared scores and alien sites gave the highest scores.

More than half of the sensitive SASS taxa (scoring eight or more) gave significantly higher mean scores in natural sites (Table 3). These included two southern and western Cape endemic families, Teloganodidae and Sericostomatidae. Helodidae, Athericidae, Corydalidae and Aeshnidae, all high-scoring SASS taxa, also gave the highest mean scores in natural sites. On the other hand, similarly sensitive taxa (scoring over ten), such as Glossosomatidae and Barbarochthonidae, both endemic to the southwestern Cape, together with Notonemouridae, contributed mostly to alien site scores. However, Table 4 shows that these taxa occurred almost exclusively in three densely alien sites along the Molenaars River and were largely absent from all other alien sites. These three sites also had a far stronger flow regime and a more cobbled substrate than were found in less-dense alien sites.

No endemic or sensitive taxa gave high scores in cleared sites, but less sensitive taxa, such as Naucoridae and Hydroptilidae, gave significantly higher SASS scores in cleared and natural sites than in alien sites.

Mean incidence was greatest in natural sites and the dense alien sites along the Molenaars River, but not significantly so (Table 4). Cleared and alien sites had similarly low levels of incidence. Taxa that occurred more frequently in natural sites than in either cleared or alien sites included mostly sensitive taxa (Aeshnidae, Corydalidae, Helodidae and Athericidae), together with Coenagrionidae and Turbellaria. The lower scoring Coenagrionidae, Hydroptilidae and Naucoridae were restricted to cleared and natural sites. Although, not always statistically significant, libellulids, naucorids, corixids, notonectids, gerrids and dytiscids, all low-scoring taxa, were encountered most frequently in cleared sites.

Caenidae and Hydraenidae had relatively high incidences in alien sites. Notonemouridae, Glossosomatidae, Barbarochthonidae and Potamonautidae occurred exclusively, or almost exclusively, in the three dense alien sites along the Molenaars River and were largely absent from the remaining alien sites. Leptophlebiids were also found mostly in these dense alien sites, being present in less than half of all other sites.

Cleared sites had the lowest incidence of sensitive families (scoring eight or more). However, the incidence of tolerant taxa (scoring less than eight) increased after alien clearing, almost matching that in natural sites. Alien sites showed a low incidence of both sensitive and tolerant taxa (although dense alien sites had a low incidence of tolerant taxa only). All endemic families had high sensitivity scores above eight.

Because of this high incidence of high-scoring SASS taxa in dense alien sites, SASS scores were recalculated for alien and dense alien sites along the Molenaars River to assess whether final SASS scores had been affected. While dense alien sites scored 147.25, alien sites scored only slightly less at 145, indicating that there was no need for separate analysis of alien and dense alien sites.

Table 1

Mean SASS (1A), ASPT (1B) and IHAS (1C) scores obtained from alien-infested, cleared and natural sites along the Rondegat and Molenaars Rivers. Subscripts indicate statistically higher values than natural ($_n$), cleared ($_c$), alien ($_a$) or Rondegat River ($_R$) sites (t-test, $P = 0.05$).

A. SASS	**Natural**	**Cleared**	**Alien**	**Overall mean (Rivers)**
	Mean ±SD	Mean ±SD	Mean ±SD	Mean ±SD $F_{1, 59} = 7.689$ ($P < 0.01$)
Molenaars River $F_{2, 28} = 1.806$ ($P = 0.184$)	130.30 ± 17.04	132.10 ± 12.45	145.30 ± 8.19	134.65 ± 20.7 $_R$
Rondegat River $F_{2, 28} = 10.220$ ($P < 0.001$)	142.10 ± 17.48 $_{c,a}$	106.80 ± 23.98	105.10 ± 19.85	117.03 ± 28.44
Overall mean (disturbance regime) $F_{2, 58} = 2.440$ ($P = 0.1$)	136.20 ± 17.85 $_c$	119.55 ± 22.62	125.20 ± 30.49	

B. ASPT	**Natural**	**Cleared**	**Alien**	**Overall mean (Rivers)**
	Mean ±SD	Mean ±SD	Mean ±SD	Mean ±SD $F_{1, 59} = 8.215$ ($P < 0.01$)
Molenaars River $F_{2, 28} = 1.644$ ($P = 0.212$)	7.09 ± 0.80	7.09 ± 0.43	7.51 ± 0.52	7.24 ± 0.61 $_R$
Rondegat River $F_{2, 28} = 5.37$ ($P < 0.050$)	7.12 ± 0.33 $_c$	6.38 ± 0.56	6.78 ± 0.58	6.81 ± 0.58
Overall mean (disturbance regime) $F_{2, 28} = 2.656$ ($P = 0.079$)	7.10 ± 0.59	6.73 ± 0.61	7.14 ± 0.66	

C. IHAS	**Natural**	**Cleared**	**Alien**	**Overall mean (Rivers)**
	Mean ±SD	Mean ±SD	Mean ±SD	Mean ±SD $F_{1, 59} = 0.107$ ($P = 0.75$)
Molenaars River $F_{2, 28} = 35.71$ ($P < 0.01$)	84.0 ± 4.99 $_a$	79.8 ± 7.42	63.0 ± 4.88	75.6 ± 10.83
Rondegat River $F_{2, 28} = 33.0$ ($P < 0.01$)	87.1 ± 3.18 $_{c,a}$	71.0 ± 8.67	66.8 ± 3.39	74.7 ± 10.39
Overall mean (disturbance regime) $F_{2, 28} = 50.39$ ($P < 0.01$)	85.6 ± 4.37 $_{c.a}$	75.0 ± 9.11 $_a$	64.9 ± 4.53	

Table 2
Mean SASS scores for alien, cleared and natural sites along five Western Cape rivers.

	Natural	**Cleared**	**Alien**	**Mean Score (Rivers)** $F_{4,9} = 10.639$ ($P < 0.01$)
Molenaars River (n = 30)	130.3	132.1	145.3	134.7
Rondegat River (n = 30)	142.1	106.8	105.1	117
Witte River (n = 2)		213	192	204.5
Holsloot River (n = 3)	164	134	139	145.7
Dwars River (n = 2)		85	58	71.5
Mean Score (disturbance regime) $F_{2,11} = 0.485$ ($P = 0.628$)	145.5	134.2	127.9	

Table 3

Mean SASS score per taxon in natural, cleared and alien sites, arranged in descending order of sensitivity (SASS score). Subscripts indicate statistically higher values than natural ($_n$), cleared ($_c$) or alien ($_a$) sites ($P = 0.05$). Asterisks indicate families endemic to the southern and western Cape.

Order	SASS Taxon	Natural Mean ± SD	Cleared Mean ± SD	Alien Mean ± SD	Sensitivity Score
Plecoptera	Notonemouridae	0.75 ± 3.13	0.61 ± 2.91	5.60 ± 7.04$_{n,c}$	14
Ephemeroptera	Heptageniidae	13.00 ± 0.00	12.43 ± 2.71	12.35 ± 2.91	13
Trichoptera	Barbarochthonidae*	0.00	0.00	0.75 ± 3.35	13
Trichoptera	Sericostomatidae*	3.25 ± 5.78$_c$	1.13 ± 3.75	2.60 ± 5.34	13
Coleoptera	Helodidae	10.80 ± 3.69$_c$	8.35 ± 5.65	9.00 ± 5.33	12
Ephemeroptera	Teloganodidae*	6.60 ± 6.13$_a$	5.74 ± 6.13	4.20 ± 5.87	12
Trichoptera	Polycentropodidae	0.00	0.00	0.60 ± 2.68	12
Trichoptera	Hydropsychidae	3.90 ± 1.02	4.09 ± 1.12	4.30 ± 0.73	4-12
Ephemeroptera	Baetidae	12.00 ± 0.00	11.13 ± 2.32	11.40 ± 1.85	4-12
Trichoptera	Glossosomatidae*	0.55 ± 2.46	0.48 ± 2.29	2.20 ± 4.51	11
Diptera	Athericidae	9.00 ± 3.08$_{c,a}$	5.22 ± 5.11	7.00 ± 4.70	10
Trichoptera	Philopotamidae	3.50 ± 4.89	1.30 ± 3.44	1.50 ± 3.66	10
Ephemeroptera	Leptophlebiidae	3.60 ± 4.52	4.30 ± 4.60	4.50 ± 4.62	9
Hydracarina	Hydracarina	1.20 ± 2.93	1.04 ± 2.76	0.00	8
Megaloptera	Corydalidae	7.20 ± 2.46$_{c,a}$	3.83 ± 4.09	4.80 ± 4.02	8
Coleoptera	Elmidae	8.00 ± 1.32	7.65 ± 1.67	8.00 ± 0.44	8
Coleoptera	Hydraenidae	1.20 ± 2.93	2.09 ± 3.59	3.60 ± 4.08$_n$	8
Trichoptera	Ecnomidae	2.40 ± 3.76	1.74 ± 3.37	1.60 ± 3.28	8
Trichoptera	Psychomyiidae	0.00	0.70 ± 2.31	0.40 ± 1.79	8
Odonata	Aeshnidae	8.00 ± 0.00$_{c,a}$	5.91 ± 3.59	6.00 ± 3.55	8
Hemiptera	Naucoridae	2.10 ± 3.29$_a$	2.43 ± 3.41$_a$	0.00	7
Hemiptera	Hydrometridae	2.10 ± 8.09	0.26 ± 1.25	0.30 ± 1.34	6
Ephemeroptera	Caenidae	4.20 ± 2.82	3.13 ± 3.07	4.80 ± 2.46$_c$	6
Trichoptera	Hydroptilidae	2.10 ± 2.94$_{c,a}$	1.83 ± 2.82$_a$	0.00	6
Trichoptera	Leptoceridae	6.00 ± 0.00	4.96 ± 2.32	5.70 ± 1.34	6
Odonata	Gomphidae	3.00 ± 3.08	4.17 ± 2.82	3.60 ± 3.01	6
Hemiptera	Gerridae	0.00	0.43 ± 1.44	0.00	5
Hemiptera	Veliidae	4.25 ± 1.83	3.70 ± 2.25	4.00 ± 2.05	5
Coleoptera	Dytiscidae	0.25 ± 1.12	0.65 ± 1.72	0.25 ± 1.12	5
Coleoptera	Gyrinidae	1.75 ± 2.45	2.83 ± 2.53	2.25 ± 2.55	5
Coleoptera	Hydrophilidae	0.00	0.22 ± 1.04	0.25 ± 1.12	5
Diptera	Ceratopogonidae	0.25 ± 1.12	1.09 ± 2.11	1.50 ± 2.35	5
Diptera	Simuliidae	4.50 ± 1.54	4.13 ± 1.94	4.00 ± 2.05	5
Diptera	Tipulidae	0.00	0.00	0.25 ± 1.12	5
Diptera	Tabanidae	1.00 ± 2.05	0.22 ± 1.04	0.75 ± 1.83	5
Odonata	Coenagrionidae	2.40 ± 2.01	1.74 ± 2.03	0.00	4
Odonata	Libellulidae	1.60 ± 2.01	2.78 ± 1.88	2.00 ± 2.05	4
Turbellaria	Turbellaria	1.20 ± 1.51	0.65 ± 1.26	0.30 ± 0.92	3
Crustacea	Potamonautidae	1.35 ± 1.53	1.04 ± 1.46	1.95 ± 1.47	3
Hemiptera	Corixidae	0.00	0.39 ± 1.03	0.15 ± 0.67	3
Hemiptera	Notonectidae	0.30 ± 0.92	0.65 ± 1.27	0.00	3
Diptera	Chironomidae	1.90 ± 0.45	1.91 ± 0.42	2.00 ± 0.00	2
Annelida	Oligochaeta	0.60 ± 0.50	0.43 ± 0.51	0.50 ± 0.51	1
Diptera	Culicidae	0.35 ± 0.49	0.13 ± 0.34	0.15 ± 0.37	1
Diptera	Muscidae	0.00	0.00	0.10 ± 0.31	1
Diptera	Psychodidae	0.05 ± 0.22	0.04 ± 0.21	0.00	1

Table 4

Mean incidence of SASS taxa in each disturbance regime, arranged in order of decreasing sensitivity (SASS score). Dense alien sites included three sites along the Molenaars River only. Subscripts indicate statistically higher values than natural ($_n$), cleared ($_c$), alien ($_a$) or dense alien ($_{da}$) sites (P = 0.05). Asterisks indicate endemic families.

	Natural (n = 20)	**Cleared** (n = 22)	**Alien** (n = 14)	**Dense Alien** (Molenaars only) (n = 6)	**TOTAL**	**Sensitivity Score**
Notonemouridae	0.10	0.04	0.21	$0.83_{n,c,a}$	1.19	14
Heptageniidae	1.00	0.91	0.93	1.00	3.84	13
Sericostomatidae*	0.25	0.09	0.29	0.00	0.62	13
Barbarochthonidae*	0.00	0.00	0.00	0.17	0.17	13
Baetidae	1.00	1.00	1.00	1.00	4.00	12
Hydropsychidae	0.95	0.96	1.00	1.00	3.91	12
Helodidae	$0.90_{c,a}$	0.70	0.64	1.00	3.24	12
Teloganodidae*	0.55	0.48	0.36	0.33	1.72	12
Polycentropodidae	0.00	0.00	0.00	0.17	0.17	12
Glossosomatidae*	0.05	0.04	0.07	$0.50_{n,c,a}$	0.66	11
Athericidae	$0.90_{c,a}$	0.52	0.57	1.00	2.99	10
Philopotamidae	0.35	0.13	0.21	0.00	0.69	10
Leptophlebiidae	0.40	0.48	0.29	$1.00_{n,c,a}$	2.16	9
Elmidae	1.00	0.96	1.00	1.00	3.96	8
Aeshnidae	$1.00_{c,a}$	0.74	0.71	0.83	3.29	8
Corydalidae	$0.90_{c,a}$	0.48	0.43	1.00	2.81	8
Hydraenidae	0.15	0.26	0.50_{n}	0.33	1.24	8
Ecnomidae	0.30	0.22	0.29	0.00	0.80	8
Hydracarina	0.15	0.13	0.00	0.00	0.28	8
Psychomyiidae	0.00	0.09	0.07	0.00	0.16	8
Naucoridae	$0.30_{a,da}$	$0.35_{a,da}$	0.00	0.00	0.65	7
Leptoceridae	1.00	0.83	0.93	1.00	3.75	6
Caenidae	0.70	0.52	0.79_{c}	0.83_{c}	2.84	6
Gomphidae	0.50	0.70	0.57	0.67	2.43	6
Hydroptilidae	$0.35_{a,da}$	$0.30_{a,da}$	0.00	0.00	0.65	6
Hydrometridae	0.10	0.04	0.07	0.00	0.21	6
Simuliidae	0.90	0.83	0.71	1.00	3.44	5
Veliidae	0.85	0.74	0.86	0.67	3.11	5
Gyrinidae	0.35	0.57	0.64	0.00	1.56	5
Ceratopogonidae	0.05	0.22	0.43	0.00	0.70	5
Tabanidae	0.20	0.04	0.21	0.00	0.46	5
Dytiscidae	0.05	0.13	0.00	0.17	0.35	5
Hydrophilidae	0.00	0.04	0.00	0.17	0.21	5
Gerridae	0.00	0.09	0.00	0.00	0.09	5
Tipulidae	0.00	0.00	0.07	0.00	0.07	5
Libellulidae	0.40	$0.70_{n,da}$	0.57	0.33	2.00	4
Coenagrionidae	$0.60_{a,da}$	$0.43_{a,da}$	0.00	0.00	1.03	4
Potamonautidae	0.45	0.35	0.50	1.00_{c}	2.30	3
Turbellaria	0.40_{a}	0.22	0.07	0.17	0.86	3
Notonectidae	0.10	0.22	0.00	0.00	0.32	3
Corixidae	0.00	0.13	0.07	0.00	0.20	3

Table 4 continued.

	Natural (n = 20)	**Cleared** (n = 22)	**Alien** (n = 14)	**Dense Alien** (Molenaars only) (n = 6)	**TOTAL**	**Sensitivity Score**
Chironomidae	0.95	0.96	1.00	1.00	3.91	2
Oligochaeta	0.60	0.43	0.50	0.50	2.03	1
Culicidae	0.35	0.13	0.14	0.17	0.79	1
Muscidae	0.00	0.00	0.07	0.17	0.24	1
Psychodidae	0.05	0.04	0.00	0.00	0.09	1
Overall mean	**0.42**	**0.38**	**0.37**	**0.41**		**1-14**
Mean (sensitive taxa)	**0.50**	**0.41**	**0.43**	**0.56**		**8-14**
Mean (tolerant taxa)	**0.36**	**0.35**	**0.32**	**0.30**		**1 - 7**

3.2. Seasonal and geographical effects on SASS scores

SASS scores varied significantly between rivers (Table 1) and seasons (Table 5). Overall, mean SASS scores were significantly higher in March than in January. However, considered individually, neither the Molenaars nor the Rondegat Rivers showed a significant difference between sampling months, although SASS scores were higher in March for both rivers.

The higher March scores occurred mainly in cleared and alien sites, natural scores remaining relatively constant across months (Table 6). These elevated March scores were statistically significant in alien sites along the Molenaars River and in cleared sites along the Rondegat River.

The only significant difference between disturbance regimes was shown in Rondegat River sites during January, with natural sites having significantly higher scores than cleared or alien sites. The difference between rivers was only significant for alien sites during March, with Molenaars River alien sites having a higher mean score than Rondegat River alien sites. It should be cautioned, however, that the subdivision of the samples reduced the power of the statistical tests and may have resulted in statistical differences not being detected (type II errors).

No consistent trends were observed across rivers, months or disturbance regimes. That is, SASS scores were not consistently highest in natural sites or lowest in alien or cleared sites, and seasonal differences were evident in cleared and alien sites but not in natural sites. Moreover, SASS scores in the Rondegat River were higher than in the Molenaars River in natural sites only, cleared and alien sites having lower SASS scores.

3.3. The effect of alien disturbance on family-level abundance

Mean total abundance of Ephemeroptera, Plecoptera, Trichoptera and Odonata was significantly higher in both natural and cleared sites than in alien sites (Table 7). Abundance was greatest in natural sites but there was no significant difference between natural and cleared sites. Analysis of

Table 5
Seasonal and geographical differences in SASS scores.

	January **Mean ± SD**	**March** **Mean ± SD**
Molenaars River $F_{1,28} = 1.11$; $P = 0.3$	129.93 ± 21.90	139.06 ± 19.14
Rondegat River $F_{1,30} = 2.98$; $P = 0.1$	108.75 ± 29.18	125.31 ± 24.92
Overall mean $F_{1,60} = 4.53$; $P < 0.05$	119.00 ± 18.39	132.19 ± 14.08

Table 6
A comparison of SASS scores across rivers, months and disturbance regimes. Subscripts indicate statistically greater values than natural ($_n$), cleared ($_c$), alien ($_a$), January ($_{Jan}$) or Rondegat River ($_R$) samples ($P = 0.05$).

	Molenaars River		**Rondegat River**	
	January	**March**	**January**	**March**
Natural	130.60 ± 22.35	130.00 ± 12.41	$142.60 \pm 8.76_{c,a}$	141.60 ± 24.69
Cleared	128.20 ± 22.54	131.67 ± 7.50	88.00 ± 25.41	$124.17 \pm 18.37_{Jan}$
Alien	131.00 ± 25.79	$159.60 \pm 18.26_{Jan, R}$	99.80 ± 11.43	110.40 ± 16.18

Table 7
Mean abundance of Ephemeroptera, Plecoptera, Trichoptera and Odonata in natural, cleared and aliens sites along five Western Cape rivers. Subscripts indicate significantly higher values than natural ($_n$), cleared ($_c$) or alien ($_a$) sites ($P = 0.05$).

	Natural Mean ± SD	**Cleared Mean ± SD**	**Alien Mean ± SD**	**Overall mean ± SD**
Ephemeroptera $F_{2,56} = 2.55$; $P = 0.09$	391.45 ± 421.15$_a$	314.36 ± 460.77	133.65 ± 123.57	280.94 ± 380.24
Trichoptera $F_{2,56} = 0.28$; $P = 0.84$	23.20 ± 15.12	20.55 ± 13.17	22.70 ± 13.18	22.14 ± 13.76
Odonata $F_{2,56} = 2.12$; $P = 0.12$	11.15 ± 5.86	13.64 ± 13.50	6.40 ± 3.39	10.50 ± 9.28
Plecoptera $F_{2,56} = 4.15$; $P < 0.05$	0.10 ± 0.31	0.09 ± 0.43	0.55 ± 0.73$_{n,c}$	0.24 ± 0.59
Mean total abundance $F_{2,58} = 1.837$; $P = 0.151$	**425.90** ± 424.59$_a$	**348.64** ± 455.46$_a$	**163.30** ± 127.23	

Table 8
Mean abundance of Ephemeroptera, Plecoptera, Trichoptera and Odonata families in natural, cleared and aliens sites along the Rondegat and Molenaars Rivers, arranged in descending order of abundance. Subscripts indicate significantly higher values than natural ($_n$), cleared ($_c$) or alien ($_a$) sites (P = 0.05). Asterisks indicate families endemic to the southern and western Cape.

	Natural ± SD (n = 20)	**Cleared ± SD** (n = 22)	**Alien ± SD** (n = 20)	**Overall mean ± SD** (n = 62)
Baetidae	134.35 ± 89.38$_a$	175.32 ± 293.05$_a$	44.80 ± 48.85	120.00 ± 189.27
Teloganodidae*	163.20 ± 291.27$_a$	77.45 ± 184.85$_a$	20.10 ± 36.61	86.61 ± 205.53
Leptophlebiidae	27.55 ± 44.90	38.00 ± 49.22$_a$	32.30 ± 20.81	32.79 ± 49.00
Heptageniidae	52.75 ± 42.48$_{c,a}$	20.32 ± 38.08	22.65 ± 45.72	31.53 ± 37.61
Caenidae	13.60 ± 17.33$_c$	3.27 ± 4.39	12.95 ± 27.68$_c$	11.84 ± 19.08
Hydropsychidae	14.70 ± 13.97$_c$	8.23 ± 7.14	13.80 ± 10.16$_c$	10 ± 10.88
Leptoceridae	6.50 ± 5.05	10.09 ± 14.14$_a$	8.45 ± 9.76	8.40 ± 10.42
Gomphidae	3.40 ± 4.93$_a$	6.59 ± 10.95	1.65 ± 2.89	3.97 ± 7.36
Aeshnidae	3.95 ± 2.96$_c$	1.91 ± 2.33	3.45 ± 1.79	3.07 ± 2.83
Libellulidae	1.25 ± 2.17	3.18 ± 4.27$_n$	1.30 ± 1.87	1.95 ± 3.11
Coenagrionidae	2.55 ± 4.05$_a$	1.95 ± 3.23$_a$	0	1.52 ± 3.14
Philopotamidae	0.80 ± 1.36	1.05 ± 4.69	0.15 ± 0.83	0.68 ± 2.89
Ecnomidae	0.35 ± 0.49	0.45 ± 0.96	0.55 ± 1.28	0.45 ± 0.95
Hydroptilidae	0.50 ± 0.83	0.50 ± 0.91	0	0.34 ± 0.75
Notonemouridae	0.10 ± 0.31	0.09 ± 0.43	0.55 ± 0.64$_{c,n}$	0.24 ± 0.59
Sericostomatidae*	0.35 ± 0.67	0.09 ± 0.29	0.20 ± 0.41	0.21 ± 0.48
Glossosomatidae*	0	0.05 ± 0.21	0.25 ± 0.37	0.10 ± 0.39
Psychomyiidae	0	0.09 ± 0.29	0.05 ± 0.22	0.05 ± 0.22
Polycentropodidae	0	0	0.05 ± 0.22	0.02 ± 0.13
Barbarochthonidae*	0	0	0.05 ± 0.22	0.02 ± 0.13
Mean total abundance $F_{2,58}$ = 1.837; P = 0.151	**425.90** ± 424.59$_a$	**348.64** ± 455.46$_a$	**163.30** ± 127.23	
Mean no. of families $F_{2,58}$ = 1.620; P = 0.19	**9.95** ± 1.82	**9.09** ± 1.31	**9.41** ± 1.40	

variance showed no overall significant difference between disturbance regimes (F = 1.837, P = 0.151).

Both the Odonata and Ephemeroptera showed a greater abundance in natural and cleared sites than in alien sites but this was only significant for Ephemeroptera. The Plecoptera were significantly most abundant in alien sites.

There was no significant difference between the mean number of families in each disturbance regime (Table 8). The Heptageniidae were significantly more abundant in natural sites than in cleared or alien sites, while the Notonemouridae were significantly most abundant in alien sites. Baetidae, Teloganodidae, Coenagrionidae and Gomphidae were significantly more abundant in both natural and cleared sites than in alien sites, while Leptophlebiidae, Leptoceridae and Libellulidae were most abundant in cleared sites. Caenidae and Hydropsychidae were more abundant in natural and alien sites than in cleared sites.

The families endemic to the southern and southwestern Cape showed varied responses. Teloganodidae and Sericostomatidae were most abundant in natural sites, teloganodids also being abundant in cleared sites. Barbarochthonidae and Glossosomatidae, on the other hand, were most abundant in alien sites and were largely absent from natural and cleared sites.

3.4. Multivariate analysis of family-level abundances

CLUSTER analysis of fourth-root transformed abundance data averaged across rivers and months showed a clear grouping of sites according to disturbance regime (Fig. 2). Cleared, natural and alien groups were identified, although some overlap did occur between them. Cleared and natural groups were most similar to each other with 81.45% similarity and there was no significant difference between them (R = 0.37, P = 1.5%). Natural sites were more similar to one another than cleared sites were. The alien group was only 79.6% similar to natural and cleared groups and

also showed the greatest variation within the group. The three dense alien sites along the Molenaars River were grouped with the remaining alien sites in the dendrogram and in the MDS ordination (Fig. 2A and B) and were therefore not differentiated from alien sites during further analyses.

The CLUSTER plot of unaveraged abundance data did not show this clear grouping according to disturbance regime (Fig. 3). Instead, the grouping was primarily according to river and, secondarily, according to month and disturbance regime. Clearly, averaging had concealed geographical and seasonal effects. ANOSIM gave a statistical significance between rivers (R = 0.582, P = 0.1%) and between months (R = 0.460, P = 0.1%), but not between disturbance regimes (R = 0.130, P = 0.2%). There was a significant difference between natural and alien groups (R = 0.194, P = 0.1%) and between cleared and alien sites (R = 0.170, P = 0.2%) but no significant difference was given between cleared and natural groups (R = 0.094 respectively, $P >$ 1%).

CLUSTER analysis of abundance data averaged across months confirmed the dominant grouping of sites according to rivers (Fig. 4). Within each river, there was a secondary grouping according to disturbance regime but, again, this was not significant (R = 0.156, P = 1%). Clearly, between-river effects needed to be excluded by analysing each river separately (Fig. 5A and 5B). The Rondegat River gave a significant difference between disturbance regimes (R = 0.433, P = 0.1%), but not between months (R = 0.094, P = 4%) (Fig 5B). The Molenaars River showed a stronger grouping according to both season and disturbance regime, with a significant difference between months (R = 0.402, P = 0.1%) and between disturbance regimes (R = 0.250, P = 0.1%) (Fig 5A). Both rivers gave a statistical difference between natural and alien and between cleared and alien groups, but differences between cleared and natural groups were not significant. To establish whether pseudoreplication (sampling sub-sites within a site) (Hurlbert, 1984) had affected results,

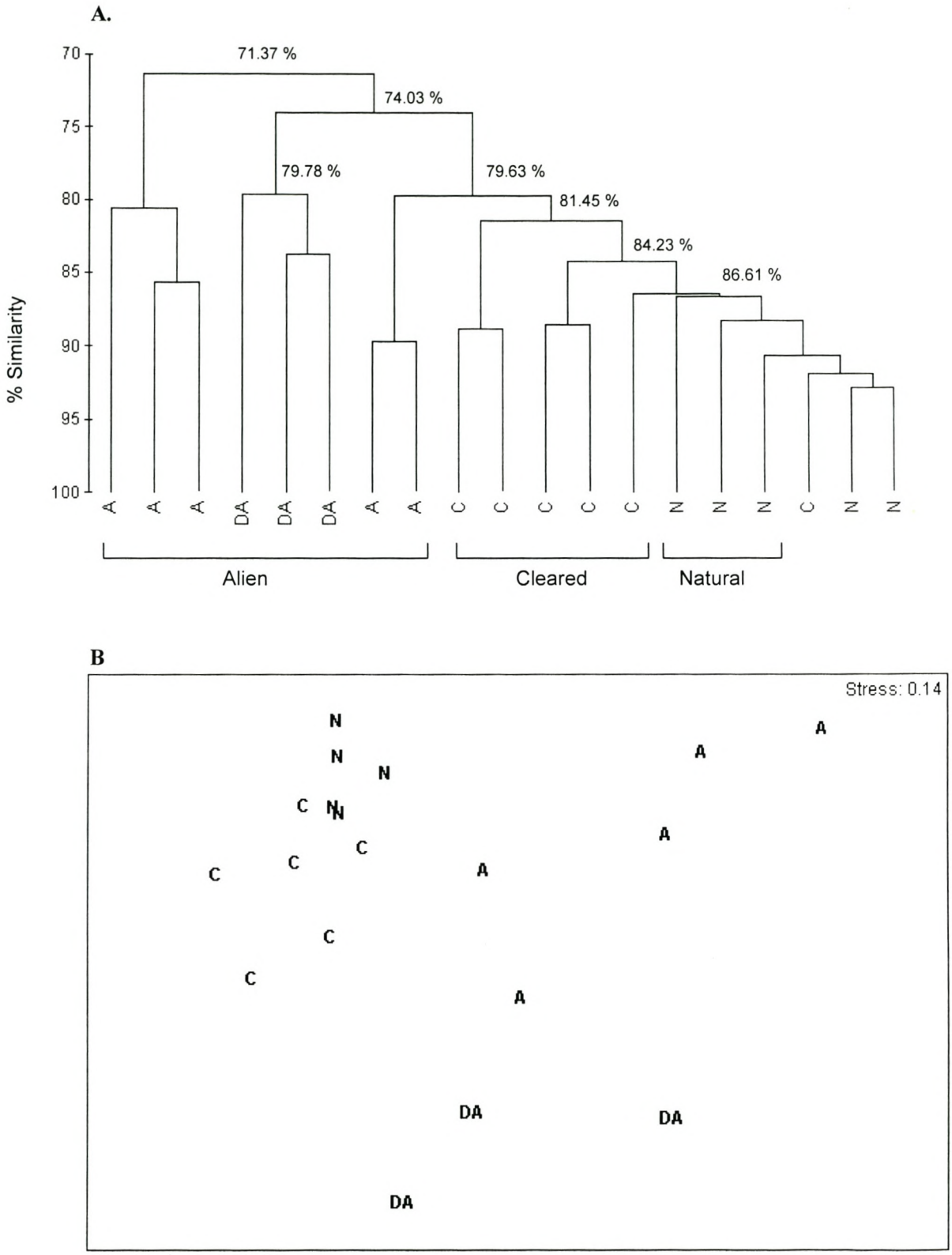


Fig. 2. A. CLUSTER dendrogram based on fourth-root transformed abundance data of Ephemeropera, Plecoptera, Trichoptra and Odonata families, averaged across rivers and months in alien, cleared and natural sites. B. MDS diagram of sites based on the CLUSTER analysis.

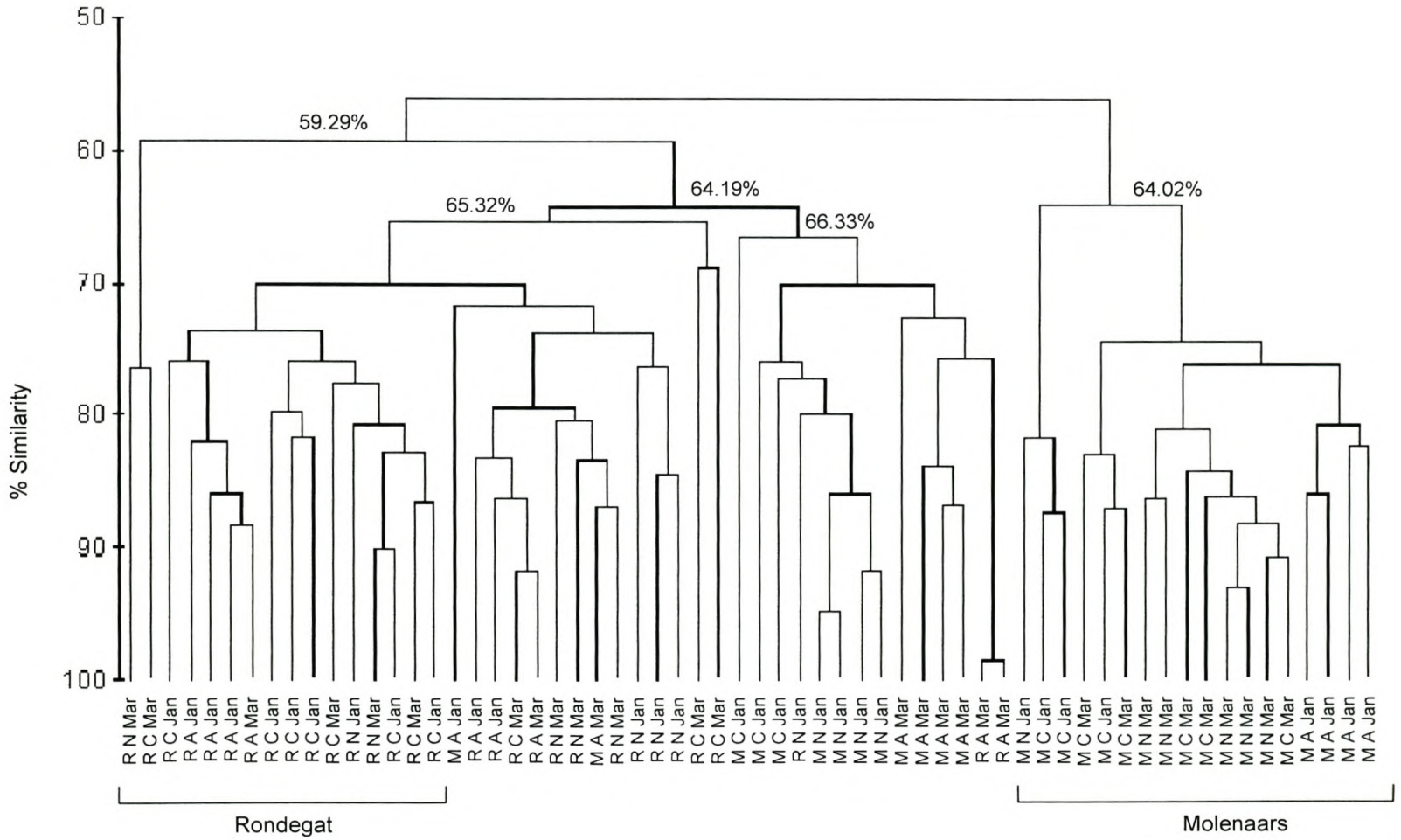


Fig. 3. CLUSTER dendrogram of fourth-root transformed abundance data of Ephemeroptera, Plecoptera, Trichoptera and Odonata families in alien (A) cleared (C) and natural (N) sites in the Molenaars (M) and Rondegat (R) Rivers during January (Jan) and March (Mar).

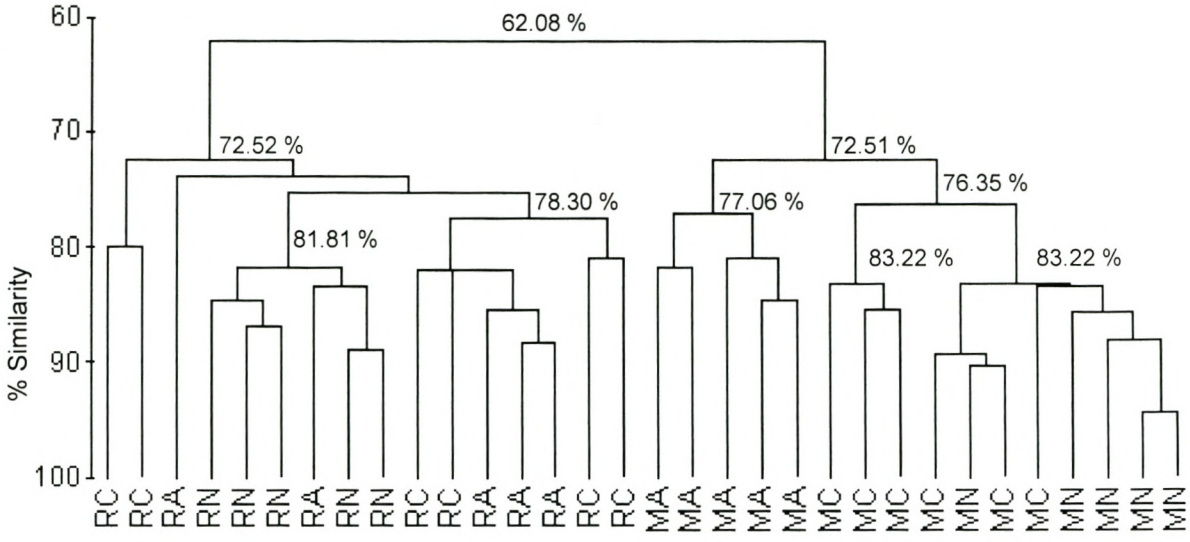


Fig. 4. CLUSTER dendrogram of fourth-root transformed abundance data of Ephemeroptera, Plecoptera, Trichoptera and Odonata families, averaged across months in alien (A) cleared (C) and natural (N) sites in the Molenaars (M) and Rondegat (R) Rivers.

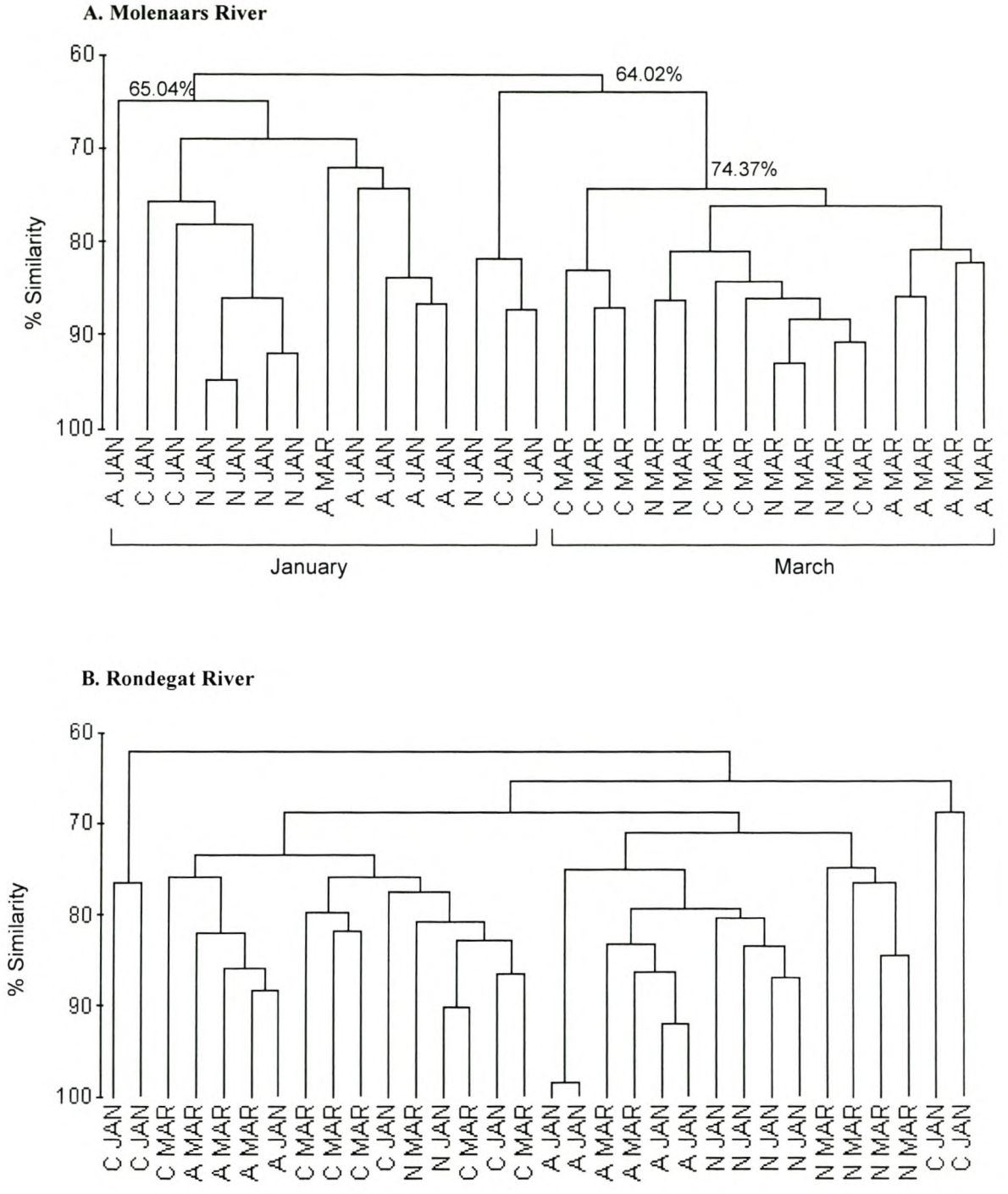


Fig. 5. CLUSTER dendrograms of the Molenaars River (A) and Rondegat River (B) showing groupings according to disturbance regime and month. N = Natural, C = Cleared, A = Alien, Jan = January, Mar = March.

ANOSIM 2 (two-way crossed design with no replication) was performed for each river. This found no global significance between sites for either river ($R < 0.147$, $P > 1\%$), suggesting that pseudoreplication may, in fact, have had some effect.

Differences between months and rivers were confirmed using analysis of variance of abundance data (Table 9). The Molenaars River had a significantly higher abundance than the Rondegat River during both months of sampling and seasonal differences were particularly evident in the Molenaars River. Abundance was always greater during March. The number of families sampled did not show major differences between rivers or between months although, overall, more families were sampled during March.

SIMPER analysis of rivers and months was used to determine which taxa were responsible for these between-river and seasonal differences (Tables 10 and 11). In particular, teloganodids and baetids were far more abundant in the Molenaars River, while caenids and gomphids were more common in the Rondegat River. Teloganodids were primarily responsible for seasonal differences, occurring almost exclusively in March. Leptophlebiids and baetids were also more abundant in March.

Because of these between-river and seasonal differences, the effects of alien disturbance on distribution patterns were analysed within each river and for each month (Table 12). Characteristic families overlapped considerably between disturbance regimes. Moreover, few families consistently characterised a particular disturbance regime in both rivers and during both months. The Baetidae were characteristic of all disturbance regimes with 15-20% contribution to overall abundance, while Heptageniidae characterised both cleared and natural sites.

Only Baetidae, Heptageniidae and Leptoceridae consistently characterised natural sites in both rivers and during both months, but they also characterised cleared and alien sites in at least one

river. Similarly, Leptophlebiidae and Hydropsychidae consistently characterised alien sites, but also characterised natural and cleared sites in at least one river. Caenidae was characteristic of Rondegat sites only and Libellulidae was characteristic of cleared sites along the Rondegat River only. The Teloganodidae were clearly characteristic of natural sites along both rivers, but only during March. Although they also occurred in alien and cleared sites along the Molenaars River during March, they were less abundant in these sites.

The CCA ordination diagram illustrates the distribution of families across sites (Fig. 6). SIMPER and CCA results are not directly comparable as CCA considers the response of relative abundance data to environmental variables, while SIMPER is based on absolute abundances independent of environmental variables. A comparison of the two, however, does give an indication of the overlap in assemblage patterns across disturbance regimes. Where such overlap occurs (e.g. Baetidae), the relative abundances of these families may be responding to factors other than alien disturbance. (The effects of environmental variables are discussed in greater detail in section 3.5.)

To remove seasonal and between-river effects 'river' and 'month' were partialled out as covariables. The CCA shows that few families were clearly associated with a particular disturbance regime. Exceptions included gomphids and libellulids, which were most abundant in cleared sites and teloganodids, which were associated mainly with natural sites. Baetids were most abundant in natural and cleared sites. Coenagrionids occurred only in cleared and natural sites (see also Tables 4 and 8). Heptageniids and sericostomatids were most abundant in natural sites, but were also associated with several alien and cleared sites.

Families responsible for distinguishing between disturbance regimes are given in Table 13. Distinguishing families differed between months and between rivers. Only baetids were consistently responsible for differences between natural and cleared sites and between natural and alien sites. In general, baetids had a higher abundance in natural sites than in cleared or alien sites,

but this was not always so; during January they were more abundant in cleared sites than in natural sites along the Molenaars River. Similarly, caenids and heptageniids were consistently responsible for differences between cleared and alien sites, but they were also not consistently most abundant in one particular disturbance regime. Libellulidae and Gomphidae were responsible for differences between natural and alien and cleared and alien sites along the Rondegat River only, while coenagrionids were responsible for these same differences, as well as differences between natural and cleared sites, along the Molenaars River only. The Teloganodidae were responsible for differences between natural and cleared and between natural and alien sites (always having a greater abundance in natural sites), but this was only consistent for both rivers during March. Where teloganodids occurred in cleared and alien sites, they were always more abundant in cleared sites than in alien sites and were considered a distinguishing species between these two disturbance regimes in the Molenaars River.

Distinguishing families are potentially useful as ecological indicators. The Indicator Value method (IndVal), which is based on both abundance and incidence, was therefore used to identify potential indicator and detector families (Table 14). No indicator families (with consistently high indicator values over 70) were identified, but several potential detectors were identified. Heptageniidae was the only family to give a consistently high indicator value (> 50) in natural sites along both rivers and during both months, thus having potential as an ecological detector of change in natural sites. Teloganodids gave particularly high indicator values (> 60) in natural sites along both rivers, but during March only. Also in March, aeshnids gave relatively high values for natural sites (47-63) and gomphids gave relatively high values (46-51) for cleared sites. In January, baetids gave high values (>50) in natural sites. Other taxa gave values that were not sufficiently high, or not sufficiently consistent, to be considered as indicators.

Table 9

Differences in abundance and richness between rivers and months.

	January Mean ± SD	**March** Mean ± SD	**Total (Rivers)** Mean ± SD
ABUNDANCE	$F_{1,27} = 7.537$ ($P < 0.05$)	$F_{1,30} = 49.51$ ($P < 0.001$)	$F_{1,58} = 27.055$ ($P < 0.001$)
Molenaars			
$F_{1,27} = 48.249$ ($P < 0.001$)	177.18 ± 76.04	851.00 ± 412.24	**533.17 ± 458.17**
Rondegat			
$F_{1,30} = 0.470$ ($P = 0.498$)	100.56 ± 53.35	115.63 ± 69.36	**108.09 ± 61.35**
Total (Months)			
$F_{1,58} = 18.267$ ($P < 0.001$)	**138.87 ± 72.82**	**483.31 ± 473.41**	
NO. OF FAMILIES	$F_{1,27} = 0.466$ ($P = 0.50$)	$F_{1,30} = 0.236$ ($P = 0.63$)	$F_{1,58} = 2.526$ ($P = 0.12$)
Molenaars			
$F_{1,27} = 0.888$ ($P = 0.355$)	8.71 ± 1.27	9.38 ± 1.53	**9.07 ± 1.41**
Rondegat			
$F_{1,30} = 3.75$ ($P = 0.062$)	9.13 ± 1.68	10.19 ± 1.41	**9.66 ± 1.62**
Total (Months)			
$F_{1,58} = 5.337$ ($P < 0.05$)	**8.93 ± 1.34**	**9.83 ± 1.66**	

Table 10

Families responsible for differences in abundance patterns between rivers, based on SIMPER analysis of fourth-root transformed abundance data obtained during January and March. Only families that cumulatively contribute up to 50% of the difference are given.

	Molenaars Mean abundance	**Rondegat** Mean abundance	**Average dissimilarity/SD**	**% contribution to total dissimilarity**
Teloganodidae*	177.60	1.31	1.23	14.65
Leptophlebiidae	64.23	67.81	1.99	11.45
Baetidae	211.63	34.09	1.44	9.41
Caenidae	5.17	14.53	1.72	9.13
Gomphidae	0.83	6.91	1.43	7.50
Heptageniidae	41.23	22.44	1.30	6.24
Libellulidae	0.73	3.09	1.25	6.04
Leptoceridae	14.27	2.91	1.19	5.71
Coenagrionidae	2.67	0.44	1.02	5.06
Aeshnidae	4.23	1.97	1.10	4.71
Hydropsychidae	8.57	14.91	1.07	3.86
Ecnomidae	0.17	0.72	0.83	3.44
Hydroptilidae	0.10	0.56	0.80	3.06

Table 11

Families responsible for differences in abundance patterns between months, based on SIMPER analysis of fourth-root transformed abundance data collected from both rivers.

	January Mean abundance	**March** Mean abundance	**Average dissimilarity/SD**	**% contribution to total dissimilarity**
Teloganodidae*	1.13	166.75	1.24	16.13
Leptophlebiidae	18.27	110.91	1.49	9.76
Baetidae	57.67	178.44	1.28	8.86
Caenidae	7.57	12.28	1.37	8.28
Heptageniidae	16.90	45.25	1.34	7.09
Gomphidae	3.47	4.44	1.22	6.88
Libellulidae	1.97	1.94	1.20	6.13
Leptoceridae	5.87	10.78	1.13	5.52
Coenagrionidae	1.03	1.97	0.97	5.12
Aeshnidae	3.13	3.00	1.03	4.86
Hydropsychidae	13.57	10.22	1.15	4.22
Ecnomidae	0.43	0.47	0.78	3.64
Hydroptilidae	0.23	0.44	0.76	3.23
Philopotamidae	1.20	0.19	0.68	3.21

Table 12

Characteristic families of natural, cleared and alien sites in the Molenaars and Rondegat Rivers during January and March. Only families contributing up to 80% of the total abundance are mentioned. Percentage contributions are given in brackets. Families that are consistently characteristic across months and rivers are italicised.

Disturbance regime	**Overall**	**Molenaars River**		**Rondegat River**	
		January	March	January	March
Natural	Teloganodidae (15.59) *Baetidae (15.03)* *Heptageniidae (11.72)* Hydropsychidae (8.31) Leptophlebiidae (8.19) Caenidae (7.48) *Leptoceridae (6.89)* Aeshnidae (6.03)	*Baetidae (24.61)* *Heptageniidae (15.96)* Leptophlebiidae (14.80) Aeshnidae (9.99) *Leptoceridae (9.39)* Coenagrionidae (8.86)	Teloganodidae (26.61) *Baetidae (20.37)* *Heptageniidae (17.58)* *Leptoceridae (9.92)* Hydropsychidae (8.86)	*Baetidae (16.90)* Hydropsychidae (14.75) *Heptageniidae (13.84)* Caenidae (11.60) *Leptoceridae (9.15)* Gomphidae (9.14)	*Baetidae (19.57)* *Heptageniidae (14.67)* Caenidae (13.29) Hydropsychidae (10.52) Teloganodidae (10.29) *Leptoceridae (8.09)*
Cleared	*Baetidae (21.85)* Leptophlebiidae (11.61) *Heptageniidae (8.56)* Leptoceridae (8.02) Hydropsychidae (8.01) Gomphidae (6.88) Libellulidae (6.67)	*Baetidae (22.56)* Leptophlebiidae (21.21) *Heptageniidae (13.27)* Hydropsychidae (12.34) Leptoceridae (12.01)	*Baetidae (24.38)* Teloganodidae (18.83) Leptophlebiidae (18.84) Leptoceridae (11.02) *Heptageniidae (7.32)*	Hydropsychidae (22.27) *Baetidae (19.13)* *Heptageniidae (17.09)* Gomphidae (15.73) Libellulidae (9.51)	*Baetidae (16.24)* Leptoceridae (12.22) Hydropsychidae (11.93) Libellulidae (9.51) Caenidae (11.47) *Heptageniidae (10.89)*
Alien	*Baetidae (14.22)* Heptageniidae (13.58) Caenidae (11.36) *Hydropsychidae (11.07)* *Leptophlebiidae (10.86)* Leptoceridae (8.54) Aeshnidae (7.28)	*Baetidae (22.06)* *Leptophlebiidae (18.88)* *Hydropsychidae (17.98)* Leptoceridae (16.86)	*Leptophlebiidae (18.31)* *Baetidae (17.57)* Heptageniidae (11.80) Leptoceridae (10.91) Teloganodidae (10.44) *Hydropsychidae (9.59)*	Heptageniidae (17.47) *Baetidae (17.02)* *Hydropsychidae (14.44)* *Leptophlebiidae (13.99)* Caenidae (74.99)	Heptageniidae (18.67) *Baetidae (17.91)* Caenidae (16.62) *Hydropsychidae (13.12)* *Leptophlebiidae (12.98)*

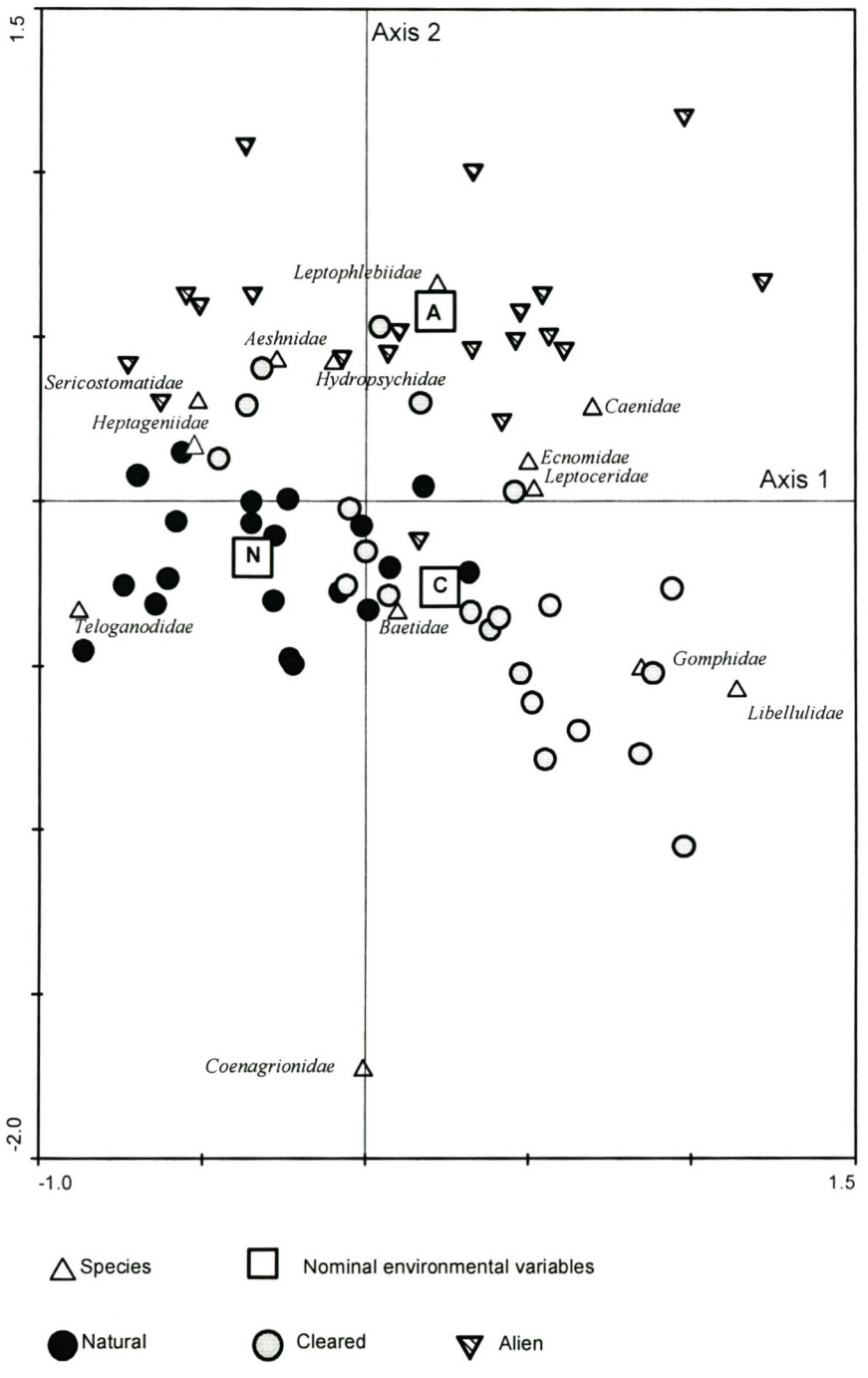


Fig. 6. CCA ordination diagram of families and sites. Axis lengths are in standard deviation units.

Table 13

Families responsible for distinguishing between natural, cleared and alien sites in the Molenaars and Rondegat Rivers during January and March. Only families responsible for up to 70% of the difference are recorded. Italicised families are consistent across rivers and months. Percentage contribution to the difference is indicated in brackets. N (natural), C (Cleared) and A (Alien) indicate the sites in which mean abundance is greater.

Disturbance regimes compared	**Overall**	**Molenaars River**		**Rondegat River**	
		January	March	January	March
Natural - Cleared	Teloganodidae (14.51) N *Baetidae (10.03) C* Leptophlebiidae (9.91) C Caenidae (8.14) N Heptageniidae (7.92) N Gomphidae (7.23) C Libellulidae (6.39) C Coenagrionidae (5.90) N	Teloganodidae (12.01) C *Baetidae (9.85) C* Philopotamidae (9.13) C Coenagrionidae (8.94) C Caenidae (8.94) C Leptophlebiidae (8.03) C Ecnomidae (6.45) C Aeshnidae (6.38) N	Leptophlebiidae (16.24) C Teloganodidae (13.85) N Heptageniidae (13.51) N Coenagrionidae (9.70) N *Baetidae (9.85) N*	Caenidae (11.43) N Leptoceridae (11.08) N Leptophlebiidae (9.59) N *Baetidae (8.27) N* Ecnomidae (7.90) N Libellulidae (7.79) C Philopotamidae (7.77) N	Teloganodidae (13.30) N *Baetidae (9.79) N* Heptageniidae (9.20) N Gomphidae (8.03) C Caenidae (7.67) N Libellulidae (7.21) C Coenagrionidae (6.03) C Aeshnidae (5.94) N
Natural - Alien	Teloganodidae (14.51) N Leptophlebiidae (9.09) A *Baetidae (8.75) N* Caenidae (8.45) A Heptageniidae (6.98) N Gomphidae (6.72) N Coenagrionidae (6.57) N Libellulidae (5.58) A	Coenagrionidae (12.52) N *Baetidae (11.61) N* Heptageniidae (11.22) N Hydropsychidae (7.51) A Notonemouridae (6.17) A Leptoceridae (6.01) A Philopotamidae (6.01) N Hydroptilidae (5.93) N	Teloganodidae (20.99) N Leptophlebiidae (12.44) C Coenagrionidae (8.80) N Heptageniidae (8.62) N Caenidae (7.49) A Notonemouridae (7.18) A *Baetidae (6.20) N*	Gomphidae (11.05) N Libellulidae (10.16) N Ecnomidae (10.14) N Philopotamidae (9.32) N Caenidae (9.00) N *Baetidae (8.70) N* Hydropsychidae (7.87) N	Teloganodidae (12.38) N *Baetidae (9.56) N* Leptophlebiidae (8.86) A Gomphidae (7.61) N Aeshnidae (77.16) N Hydroptilidae (6.69) N Libellulidae (6.68) N Ecnomidae (6.68) A Coenagrionidae (6.45) N
Cleared - Alien	Teloganodidae (11.60) C Baetidae (10.41) C Leptophlebiidae (8.75) C *Caenidae (8.52) A* Gomphidae (7.20) C *Heptageniidae (6.91) A* Libellulidae (6.65) C Leptoceridae (6.57) C	Teloganodidae (10.95) C *Caenidae (8.82) C* Coenagrionidae (12.52) N Leptophlebiidae (13.65) A Aeshnidae (6.38) N Baetidae (7.60) C *Heptageniidae (11.08) C* Notonemouridae (6.17) A	Baetidae (13.82) C Teloganodidae (12.85) C *Heptageniidae (9.68) C* Notonemouridae (9.36) A Coenagrionidae (9.16) C *Caenidae (7.98) A* Glossosomatidae (5.92) A	Leptophlebiidae (13.79) A *Caenidae (9.98) A* Gomphidae (9.75) C Leptoceridae (9.13) A Libellulidae (9.01) C Aeshnidae (8.97) A *Heptageniidae (6.86) A*	Gomphidae (10.76) C Hydroptilidae (10.55) C *Heptageniidae (10.39) A* Libellulidae (9.03) C *Caenidae (8.61) A* Ecnomidae (7.76) A Leptophlebiidae (7.35) A Aeshnidae (6.30) C

Table 14

Potential indicator and detector families (in bold) as indicated by their indicator values (in brackets) in alien, cleared and natural sites during January and March in the Molenaars and Rondegat Rivers. Families with consistently high indicator values are italicised.

	Overall	**Molenaars River**		**Rondegat River**	
		January	**March**	**January**	**March**
Natural	***Heptageniidae (55.11)***	***Heptageniidae (67.36)***	**Teloganodidae (64.12)**	**Leptoceridae (69.57)**	**Teloganodidae (93.23)**
	Aeshnidae (42.43)	**Baetidae (58.13)**	***Heptageniidae (56.83)***	**Caenidae (62.49)**	**Baetidae (71.09)**
	Hydropsychidae (38.92)	Coenagrionidae (42.62)	Aeshnidae (46.65)	**Baetidae (60.14)**	**Aeshnidae (62.79)**
	Baetidae (37.91)	Aeshnidae (44.68)	Coenagrionidae (40.94)	**Hydropsychidae (56.12)**	**Caenidae (53.83)**
	Teloganodidae (34.44)			***Heptageniidae (50.15)***	***Heptageniidae (52.59)***
Cleared	Baetidae (49.46)	**Teloganodidae (54.25)**	**Baetidae (61.55)**	Gomphidae (48.98)	**Libellulidae (62.50)**
	Gomphidae (41.17)	**Leptophlebiidae (53.63)**	Leptoceridae (48.76)	Libellulidae (40.32)	**Gomphidae (51.13)**
	Libellulidae (40.37)	Ecnomidae (41.67)	Gomphidae (46.29)	Hydroptilidae (35.71)	Hydroptilidae (43.86)
Alien	Hydropsychidae (36.10)	Hydropsychidae (63.11)	Hydropsychidae (38.46)	Aeshnidae (41.59)	**Leptophlebiidae (68.63)**
	Caenidae (35.99)	**Leptoceridae (54.48)**	Leptophlebiidae (33.20)	Heptageniidae (38.05)	Hydropsychidae (45.63)
	Leptophlebiidae (33.01)				Heptageniidae (40.71)
	Leptoceridae (32.07)				Caenidae (40.15)

3.5. Environmental effects on family distribution patterns

CCA indicated a strong invertebrate-environment correlation (greater than 0.75 on all axes) and the environmental variables measured were responsible for the main variation in family distribution patterns (cumulative percentage variance of invertebrate data and invertebrate-environment relations = 85.4%). The total inertia was 0.69. The Monte Carlo test confirmed that the measured environmental variables accounted for a significant amount of variation of the first axis ($F = 23.95$, $P = 0.002$) and the overall ordination ($F = 4.28$, $P = 0.002$).

The Monte Carlo permutation test of each variable considered individually (marginal effects) found that the most important environmental variables to affect distribution patterns included river system, width, depth, conductivity, temperature and month of sampling (Table 15). Disturbance regime and percentage alien trees were less important. Alien trees were co-correlated with coarse particulate organic matter (CPOM) (mainly plant debris) and percentage canopy cover ($r > 0.795$). These three variables were therefore collectively considered as a single variable.

The Monte Carlo test of variables progressively included by forward selection (conditional effects) confirmed the overriding effects of river and month (Table 15). Also statistically significant were width, indigenous bushes, dissolved oxygen, *Prionium* and alien trees ($P < 0.05$).

To factor out the effects of river and season, a partial CCA was performed with 'river' and 'month' treated as covariables (Table 16). With these effects removed, the most important environmental variables, in descending order of importance, included width, indigenous bushes, bank exposure, disturbance regime, *Prionium*, temperature, dissolved oxygen and flow. Considered collectively (conditional effects), only width, indigenous bushes, dissolved oxygen, *Prionium*, alien trees (which included CPOM and canopy cover) and bank exposure were statistically significant ($P < 0.05$).

The Monte Carlo test of the partial CCA again confirmed that the measured environmental variables accounted for a significant amount of variation of the first axis ($F = 8.102$, $P = 0.01$) and the overall ordination ($F = 2.25$, $P = 0.002$). The invertebrate-environment correlation was strong (greater than 0.71 on all axes) and the environmental variables were responsible for the main variation in invertebrate distribution patterns (cumulative percentage variance of invertebrate data and invertebrate-environment relations = 86%). The total inertia was 0.69.

The ordination diagram of the partial CCA shows the clear grouping of sites according to disturbance regime (Fig. 7). Alien sites were strongly associated with alien tree cover and exposed banks (i.e. an absence of marginal vegetation). Conversely, natural and cleared sites were associated with high levels of cover of indigenous bushes, *Prionium* and sedge (and grass). Cleared sites were also associated with high temperatures, conductivity and suspended solid concentrations. Natural sites tended to be wider and deeper, while strong flow rates occurred mainly in natural and alien sites (in particular, the three dense alien sites along the Molenaars River). The arrow lengths clearly indicate the importance of indigenous bushes, *Prionium*, alien cover and bank exposure. The arrow for width is somewhat shorter but this is because width was mainly correlated to the fourth and fifth axes and this information was lost during the conversion of multidimensional data to a two dimensional plot. Axis 1 was more important than axis 2 in explaining the observed distribution patterns (eigenvalues 0.26 and 0.07 respectively). Bank exposure was strongly correlated to axis 1, while *Prionium*, alien trees and indigenous bushes were strongly correlated to the second axis.

Fig. 8 gives the response of the most common families to each environmental variable, as well as their distribution patterns across disturbance regimes (represented as centroids). Philopotamidae, Hydroptilidae and Notonemouridae were outliers and were therefore excluded from the ordination diagram. Baetids, gomphids and libellulids were associated with warmer cleared sites. Gomphids and libellulids were also associated with sand and gravel substrates and an abundance of

Table 15

Environmental variables, in descending order of importance in affecting family-level abundance patterns, as indicated by their eigenvalues. *P* = significance level of the fit as obtained from the Monte Carlo Permutation test with each variable considered individually (marginal effects) and collectively by forward selection (conditional effects). Canopy cover and percentage alien trees were strongly co-correlated and therefore considered as a single variable.

	Marginal effects			**Conditional effects (Forward selection)**	
	Eigenvalues	***P***		**Eigenvalues**	***P***
River	0.21	0.002	River	0.21	0.002
Width	0.13	0.002	Month	0.05	0.002
Depth	0.13	0.002	Width	0.03	0.002
Conductivity	0.12	0.002	Indigenous bushes (%)	0.03	0.002
Temperature	0.08	0.002	Dissolved oxygen	0.03	0.002
Month	0.08	0.002	*Prionium* (%)	0.02	0.002
Prionium (%)	0.07	0.002	Alien/ Canopy cover (%)	0.01	0.012
Sedge/grass (%)	0.06	0.002			
Indigenous bushes (%)	0.06	0.004			
Flow	0.05	0.002			
Bank exposure (%)	0.05	0.002			
Gravel (%)	0.04	0.010			
Dissolved oxygen	0.04	0.020			
Cobbles (%)	0.03	0.020			
Disturbance Regime	0.03	0.020			
Sand (%)	0.03	0.020			
Alien/ Canopy cover (%)	0.02	> 0.05			
pH	0.02	> 0.05			
Riffle (%)	0.02	> 0.05			
TSS	0.02	> 0.05			
Pool (%)	0.01	> 0.05			

Table 16

Environmental variables, in descending order of importance in affecting abundance patterns, as indicated by their eigenvalues. The geographical and seasonal effects were partialled out by taking the variables 'river' and 'month' as covariables. *P* = significance level of the fit as obtained from the Monte Carlo Permutation test with each variable considered individually (marginal effects) and collectively by forward selection (conditional effects). Canopy cover and percentage alien trees were strongly co-correlated and therefore considered as a single variable.

	Marginal effects			**Conditional effects (Forward selection)**	
	Eigenvalues	***P***		**Eigenvalues**	***P***
Width	0.03	0.03	Width	0.03	0.004
Indigenous bushes (%)	0.03	0.03	Indigenous bushes (%)	0.03	0.002
Bank exposure	0.03	0.03	Dissolved oxygen	0.03	0.014
Disturbance regime	0.03	0.03	*Prionium* (%)	0.02	0.002
Prionium (%)	0.03	0.03	Alien/ Canopy cover (%)	0.01	0.042
Dissolved oxygen	0.03	0.03	Bank exposure	0.01	0.044
Depth	0.02	0.02			
Alien/ Canopy cover (%)	0.02	0.02			
Flow	0.02	0.02			
Sedge/grass (%)	0.02	0.02			
Sand (%)	0.02	0.02			
Gravel (%)	0.01	0.01			
Pool (%)	0.01	0.01			
Cobbles (%)	0.01	0.01			
Temperature	0.01	0.01			
pH	0.01	0.01			
TSS	0.01	0.01			
Conductivity	0.01	0.01			
Riffles (%)	0.01	0.01			

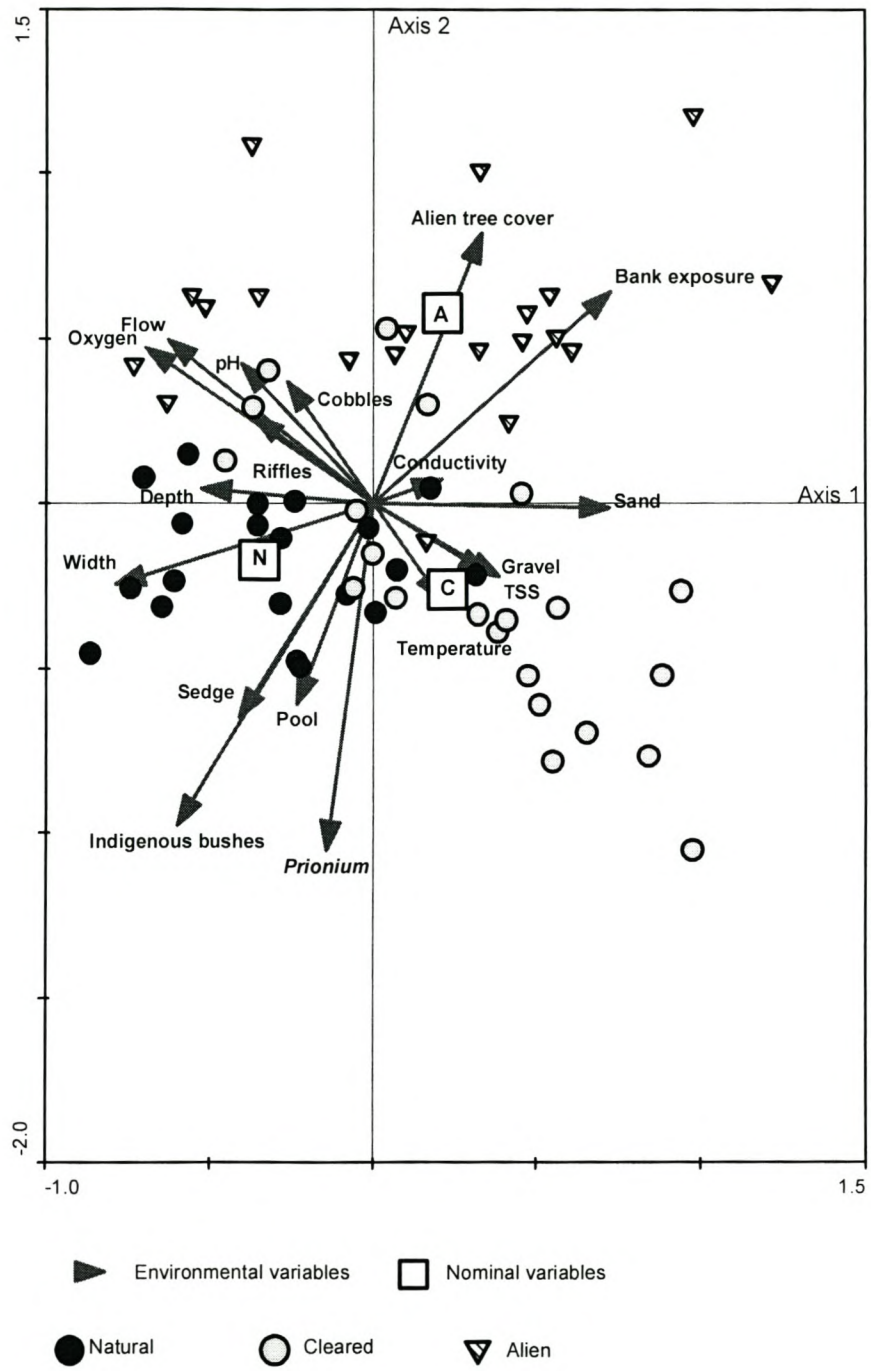


Fig. 7. CCA ordination diagram of sites and environmental variables affecting family distribution patterns across disturbance regimes in the two rivers. The variance accounted for by the first two axes was 67.8%. Eigenvalues were 0.26 and 0.07 on axes 1 and 2 respectively.

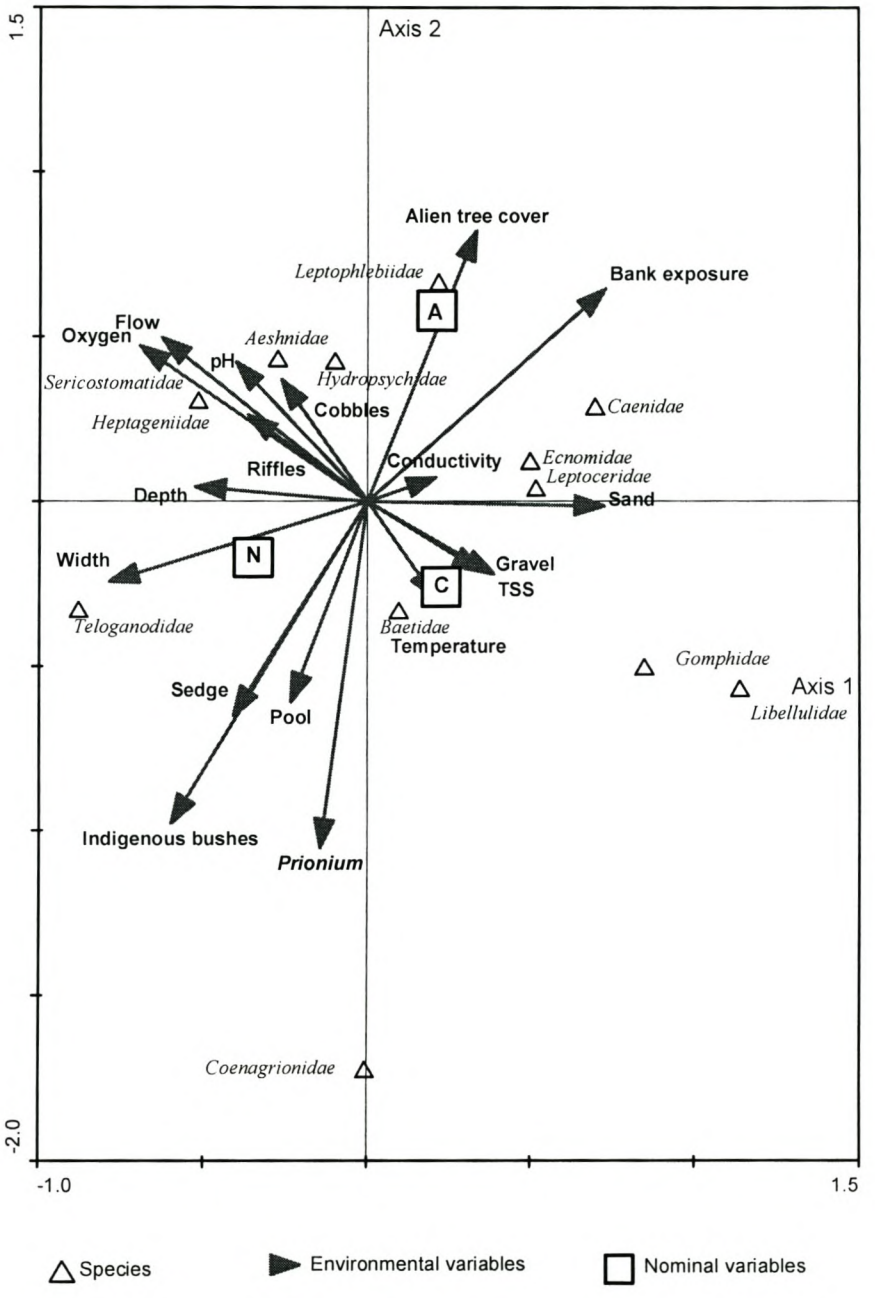


Fig. 8. CCA ordination diagram of environmental variables affecting the distribution patterns of the most common families across sites. Sites within each disturbance regime are represented as centroids (N = natural, C = cleared and A = alien).

Prionium. Coenagrionids were clearly associated with abundant *Prionium* growth, as well as with an abundance of indigenous bushes, grass and sedge. Coenagrionids tended to occur in the warmer cleared and natural sites that had pools and gravel substrates. Teloganodids were clearly associated with wide, deep natural sites with an abundance of indigenous bushes. Sericostomatids, heptageniids, aeshnids and hydropsychids were associated with high flow rates and cobbled substrates. Ecnomids, leptocerids and caenids were associated with sand and gravel substrates in cleared and alien sites, while leptophlebiids and caenids were associated with alien trees and exposed banks in alien sites.

3.6. Analysis of morphospecies abundance data

The number of morphospecies identified did not differ significantly between disturbance regimes ($F = 1.84$, $P = 0.15$) but was slightly lower in alien sites (Table 17). (Please note that all genus and species names given to morphospecies are tentative and require confirmation by an expert.)

L. penicillata (the only representative of the Teloganodidae), *Baetis harrisoni*, *Pseudocloeon bellum*, *Demorepus capensis* (all Baetidae) and *Pseudagrion* A (Coenagrionidae) all had higher mean abundances in natural and cleared sites, than in alien sites. *Afronurus harrisoni* (the only morphospecies within the Heptageniidae) and baetid C had the highest mean abundances in natural sites. Baetid B and *Chloroterpes* B (Leptophlebiidae) had high abundances in cleared sites, while *Caenis capensis* (the only representative of the Caenidae), *Aeshna* sp. (Aeshnidae) and *Cheumatopsyche* sp. (Hydropsychidae) had the lowest abundances in cleared sites.

Of the species endemic to the southern and southwestern Cape, *L. penicillata*, *Athripsodes* C, *Petroplax* sp., *Aeshna* sp. (probably *A. subpupillata*) and *Pseudagrion* A (probably *P. furcigerum*) were most abundant in natural sites. *Athripsodes* C and *Aeshna* sp. were also fairly common in alien sites but were considerably less abundant in cleared sites. *Leptecho helicotheca* was abundant only in natural and cleared sites. Only *Athripsodes* C and *Orthetrum* sp. (probably *O.*

julia capicola) were most abundant in cleared sites, while *Athripsodes* A and B, together with *Agapetus* sp. and *Barbarochthon brunneum*, were most abundant in alien sites. Few of these differences were, however, statistically significant.

Species accumulation curves derived from morphospecies data indicated pronounced differences between the two rivers (Fig. 9B and 9C). Cleared sites had the lowest abundance in the Rondegat River, but the highest abundance in the Molenaars River. The number of morphospecies was greatest in natural sites in the Rondegat River, but in cleared sites in the Molenaars River. Alien sites in the Rondegat River had the lowest number of morphospecies, while in the Molenaars River, the number of morphospecies matched that of natural sites although alien sites had the lowest abundance. Overall (Fig 9A), alien sites had the lowest abundance and number of morphospecies. Cleared sites had the greatest number of morphospecies and natural sites had the greatest abundance.

CLUSTER analysis of sites according to morphospecies abundance again showed the dominant effect of river and season. However, the morphospecies level of identification appeared to have a greater ability to classify sites than family-level abundances. This time, ANOSIM gave an overall significant difference between disturbance regimes (R = 0.16, 0.1%) and, within each river, all disturbance regimes were significantly different, except natural and cleared groups in the Molenaars River (R = 0.10, P = 7.7%).

MDS ordination diagrams of sites showed a very strong grouping according to rivers (Fig. 10A) but not according to disturbance regime (Fig. 10B). Cleared and alien sites, in particular, showed great variability, while natural groups were more defined. Sites were also grouped according to dominant vegetation type (Fig. 10C). Indigenous bush and *Prionium* groups were clearly evident. Dominant vegetation in cleared sites ranged from grass and *Prionium* through to short and tall indigenous bushes and fynbos. Natural sites, on the other hand, had only indigenous bushes and

Table 17
Mean abundance of Ephemeroptera, Plecoptera, Trichoptera and Odonata, identified to morphospecies, in natural, cleared and aliens sites along the Rondegat and Molenaars Rivers. Morphospecies are arranged in descending order of abundance. Where species names are given, these are tentative and for convenience purposes only, pending confirmation by specialists. Subscripts indicate significantly higher values than natural ($_n$), cleared ($_c$) or alien ($_a$) sites (P = 0.05). Asterisks indicate families endemic to the southern and western Cape.

	Natural Mean ± SD n = 20	**Cleared** Mean ± SD n = 22	**Alien** Mean ± SD n = 20	**Overall Mean** n = 62
EPHEMEROPTERA				
*Lestagella penicillata**	163.20 ± 291.27$_a$	77.45 ± 184.85$_a$	20.10 ± 45.72	86.61
Baetis harrisoni	74.75 ± 50.84$_a$	133.09 ± 259.38$_a$	30.90 ± 42.24	81.31
Afronurus harrisoni	52.75 ± 42.48$_{c,a}$	20.32 ± 38.08	22.65 ± 20.81	31.53
Euthraulus elegans	17.00 ± 36.89	23.00 ± 33.94	16.55 ± 23.28	18.98
Pseudocloeon bellum	27.55 ± 34.88$_a$	18.18 ± 25.63$_a$	1.05 ± 1.32	15.68
Caenis capensis	13.60 ± 17.3$_c$	3.27 ± 4.39	13.80 ± 27.68$_c$	10.00
Adenophlebia spp.	7.05 ± 10.62	9.91 ± 15.69	11.70 ± 15.28	9.57
Demorepus capensis	9.75 ± 4.85$_a$	9.50 ± 13.12$_a$	4.75 ± 6.99	8.05
Baetid sp. C	11.15 ± 8.76$_{c,a}$	5.77 ± 5.42	3.55 ± 3.80	6.79
Baetidae sp. E	5.15 ± 4.56	3.05 ± 4.77	1.45 ± 2.24	3.21
Chloroterpes elegans	2.25 ± 2.67	3.32 ± 5.46	2.40 ± 3.19	2.68
Baetidae spp.	3.85 ± 5.51$_a$	2.41 ± 3.08$_a$	0.10 ± 0.45	2.13
Baetidae sp. A	1.00 ± 1.62	1.32 ± 2.83	1.95 ± 3.61	1.42
Acanthiops sp.	0.75 ± 1.45	1.27 ± 1.61	1.05 ± 1.47	1.03
Leptophlebiidae spp.	1.05 ± 3.55	1.00 ± 1.72	0.75 ± 1.80	0.94
Chloroterpes sp. B	0.20 ± 0.52	0.77 ± 2.43$_n$	0.90 ± 3.57	0.63
Baetidae sp. B	0.40 ± 1.23	0.73 ± 3.19$_a$	0.00	0.39
TRICHOPTERA				
Cheumatopsyche sp.	14.65 ± 13.98$_c$	8.09 ± 7.10	12.80 ± 10.22$_c$	11.73
Athripsodes bergensis group sp. C*	4.20 ± 5.43	7.86 ± 13.15$_n$	5.50 ± 6.74	5.92
Athripsodes sp. C*	1.15 ± 1.23	0.50 ± 0.60	0.95 ± 1.05	0.85
Chimarra sp.	0.80 ± 1.36	1.05 ± 4.69	0.15 ± 0.37	0.68
Athripsodes bergensis group sp. B*	0.05 ± 0.22	0.36 ± 1.50	1.05 ± 2.91	0.48
Athripsodes sp. B	0.50 ± 0.89	0.41 ± 0.73	0.20 ± 0.69	0.37
Ecnomus sp.	0.25 ± 0.44	0.27 ± 0.77	0.55 ± 1.28	0.36
Hydroptila capensis	0.50 ± 0.83	0.45 ± 0.74	0.00	0.32
*Leptecho helicotheca**	0.40 ± 0.75	0.41 ± 0.85	0.05 ± 0.22	0.29
Athripsodes bergensis group sp. A*	0.10 ± 0.31	0.09 ± 0.29	0.50 ± 0.95	0.23
Petroplax sp.*	0.35 ± 0.67	0.09 ± 0.29	0.20 ± 0.41	0.21
Macrostemum sp.	0.05 ± 0.22	0.14 ± 0.35	0.15 ± 0.37	0.11
Athripsodes harrisoni group sp. C	0.00	0.18 ± 0.39	0.15 ± 0.37	0.11
Agapetus sp.*	0.00	0.05 ± 0.21	0.25 ± 0.64	0.09
Parecnomina resima	0.10 ± 0.31	0.18 ± 0.67	0.00	0.09
Athripsodes harrisoni group sp. D	0.05 ± 0.22	0.14 ± 0.47	0.05 ± 0.22	0.08
Paduniella capensis	0.00	0.09 ± 0.29	0.05 ± 0.22	0.05
Athripsodes harrisoni group sp. A	0.05 ± 0.22	0.09 ± 0.21	0.00	0.05
Oxyethira velocipes	0.00	0.05 ± 0.21	0.00	0.02
Paranyctiophylax sp.	0.00	0.00	0.05 ± 0.22	0.02
Athripsodes harrisoni group sp. B	0.00	0.05 ± 10.95	0.00	0.02
*Barbarochthon brunneum**	0.00	0.00	0.05 ± 0.22	0.02

Table 17 continued

	Natural Mean ± SD n = 20	**Cleared** Mean ± SD n = 22	**Alien** Mean ± SD n = 20	**Overall Mean** n = 62
ODONATA				
Paragomphus (*cognatus*)[1]	3.35 ± 4.90	6.59 ± 10.95	1.60 ± 1.67	3.94
Aeshna (*subpupillata*)*	3.75 ± 2.88$_c$	1.77 ± 2.35	3.45 ± 2.89	2.95
Pseudagrion sp. A (*furcigerum*)*	2.15 ± 3.53$_a$	0.86 ± 1.61$_a$	0.00	1.00
Trithemis sp. A (*furva*)	0.85 ± 1.50	1.36 ± 2.72	0.55 ± 1.40	0.94
Orthetrum (*julia capicola*)*	0.25 ± 0.79	1.27 ± 2.33	0.20 ± 0.52	0.60
Pseudagrion sp. B	0.35 ± 0.67	1.00 ± 1.95	0.00	0.47
Zygonyx (*natalensis*)	0.10 ± 0.31	0.36 ± 0.73	0.50 ± 0.95	0.32
Anax (*speratus* / *imperator*)	0.20 ± 0.41	0.14 ± 0.35	0.00	0.11
Trithemis sp. B (*arteriosa*)	0.05 ± 0.22	0.18 ± 0.85	0.05 ± 0.22	0.10
Ceriagrion (*glabrum*)	0.05 ± 0.22	0.09 ± 0.29	0.00	0.05
Ceratogomphus sp.	0.05 ± 0.22	0.00	0.05 ± 0.22	0.03
NOTONEMOURIDAE	0.10 ± 0.31	0.09 ± 0.43	0.55 ± 0.84	0.24
Mean overall abundance (sites) $F_{2,58} = 1.837$, $P = 0.151$	**425.90** ± 424.59$_a$	**348.64** ± 455.46$_a$	**163.30** ± 127.23	
Mean no. of morphospecies $F_{2,58} = 1.838$, $P = 0.150$	**17.70** ± 2.77	**16.41** ± 4.96	**15.71** ± 1.97	
Total no. of morphospecies	**46.00**	**48.00**	**43.00**	

[1] Brackets indicate probable species names as indicated by the presence of adults.

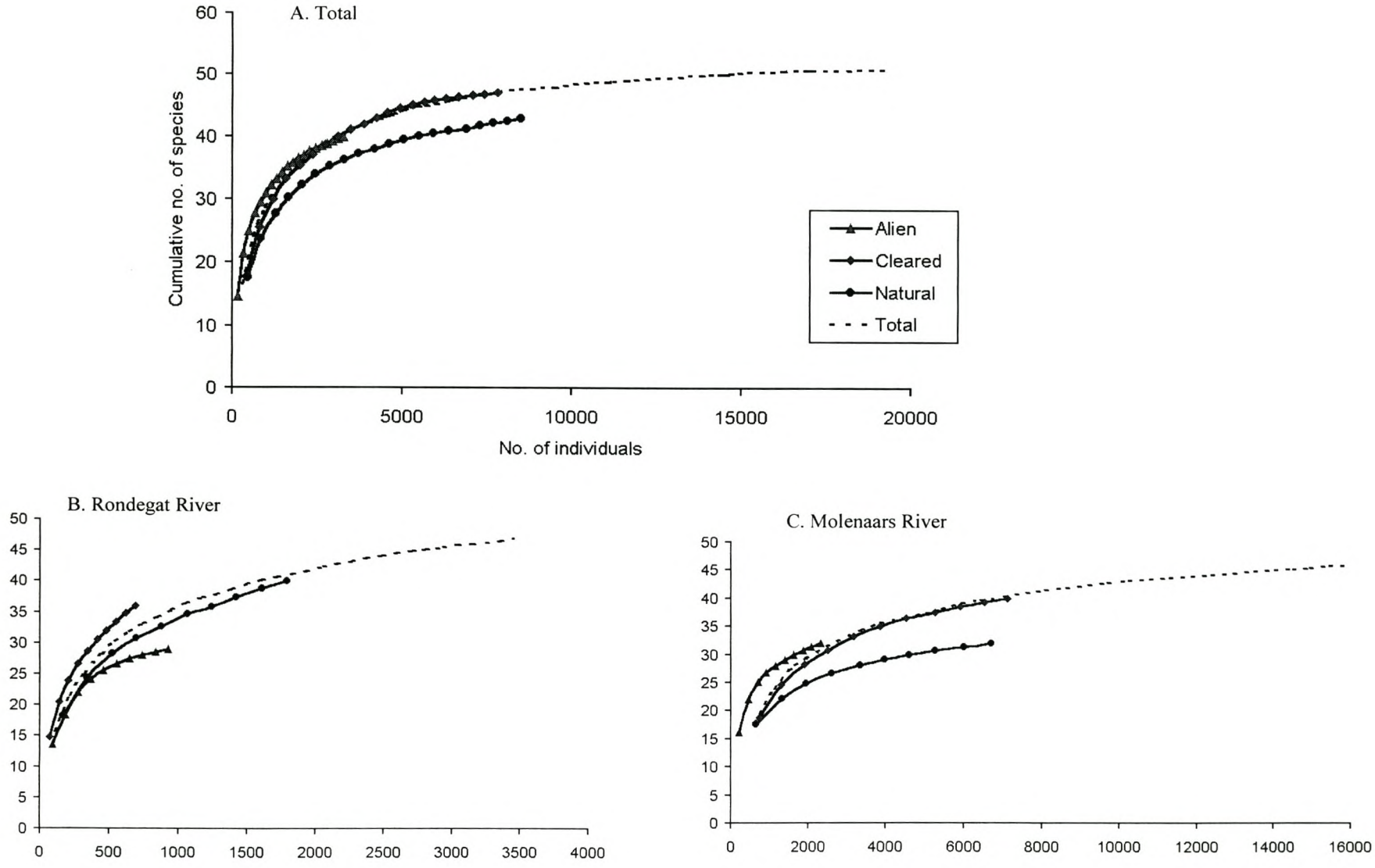


Fig. 9. Species accumulation curves for Ephemeroptera, Plecoptera, Trichoptera and Odonata morphospecies sampled from natural, cleared and alien sites in the Rondegat (A) and Molenaars (B) rivers during January and March. Twenty samples were sampled from each disturbance regime, ten in each river.

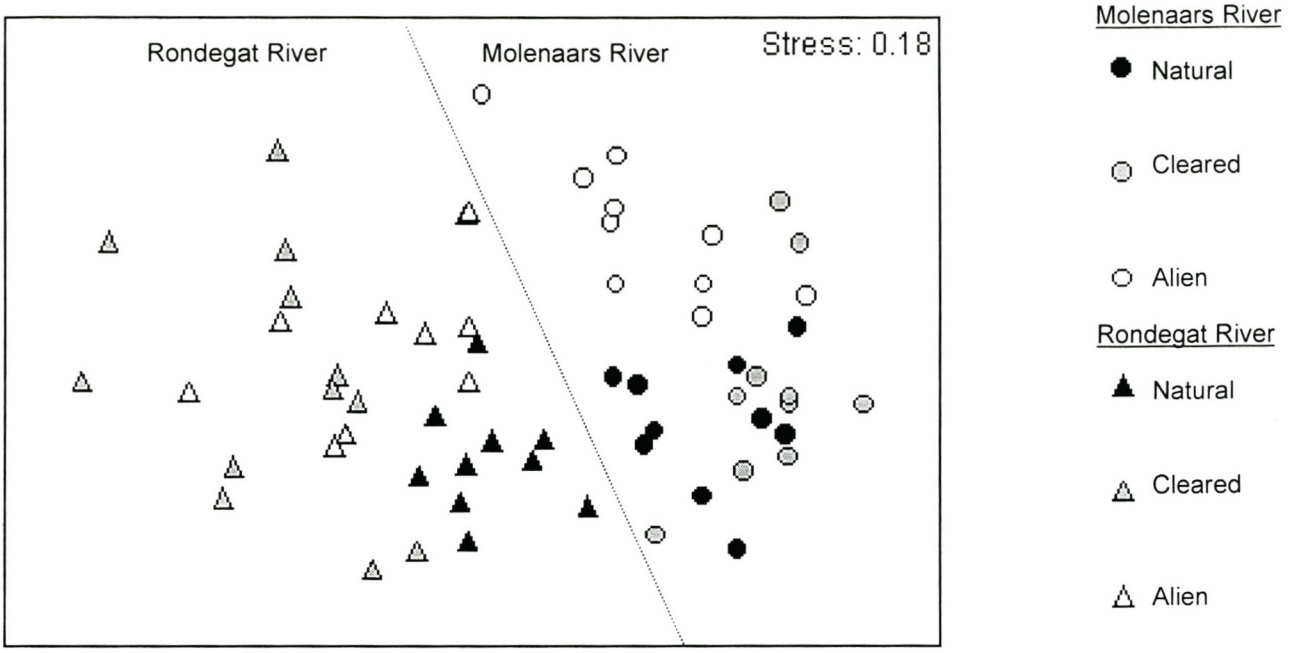


Fig. 10. MDS diagram of sites based on morphospecies abundance showing grouping according to rivers and alien disturbance regime. Circles indicate Molenaars River sites and triangles indicate Rondegat River sites.

trees or *Prionium* as dominant vegetation type, grass never dominating in these sites. Therefore, cleared sites with indigenous bushes as dominant vegetation type were most similar to natural sites. These were followed by cleared sites with an abundance of *Prionium*. Cleared sites dominated by grass and sedge tended to be outliers and were the least similar to natural sites.

Fig. 11 shows that, in both rivers, natural sites were relatively similar to one another, while cleared and alien sites were highly variable and widely distributed in the MDS. The MDS also shows the similarity between cleared and natural sites in the Molenaars River and between cleared and alien sites in the Rondegat River.

Morphospecies responsible for seasonal and between-river differences are listed in Tables 18 and 19. *L. penicillata* (the only species within the Teloganodidae) was primarily responsible for these differences, as was already shown by the family-level analysis (Tables 10 and 11). *Euthraulus elegans* also differed greatly between rivers and months. Most morphospecies were more abundant in the Molenaars River than the Rondegat River, with only *Caenis capensis* and *Paragomphus* sp. being more abundant in the Rondegat Rivers. All distinguishing morphospecies were more abundant in March than in January.

SIMPER analysis of morphospecies data again showed great overlap between characteristic assemblages in each disturbance regime (Table 20). There was also little consistency across rivers and months, although *B. harrisoni* and *A. harrisoni* were consistently characteristic of all three disturbance regimes in both rivers and during both months. Baetid 'C' and *P. bellum* were characteristic of all natural sites, while *Cheumatopsyche* sp. was consistently characteristic of alien sites. However, all overlapped with other disturbance regimes in at least one river.

When only March was considered, *L. penicillata*, *P. bellum* and *Cheumatopsyche* sp. characterised natural sites in both rivers and *E. elegans* was characteristic of alien sites. However,

only *L. penicillata* showed little overlap with other disturbance regimes, having a markedly higher abundance in natural sites.

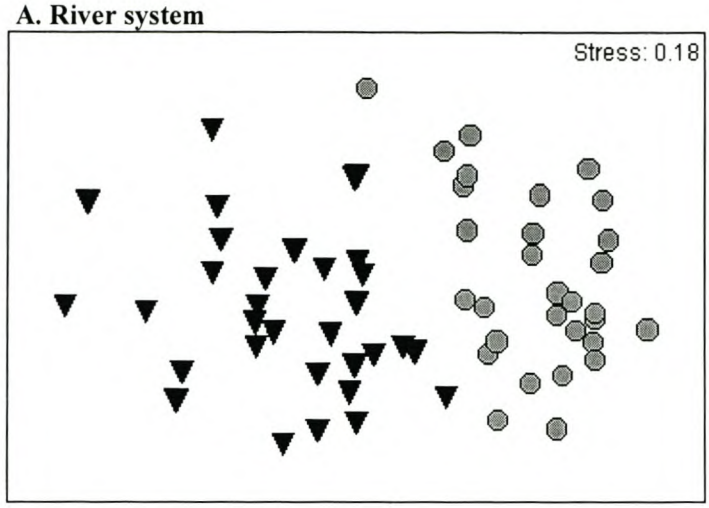
With the exception of the baetids, *P. bellum* and baetid C, these characteristic morphospecies were either the most abundant representative of their families (i.e. *Cheumatopsyche* sp., *E. elegans*, *B. harrisoni*) or the only morphospecies within their family (i.e. *L. penicillata*, *A. harrisoni*). It is likely, therefore, that analysis at family level would give sufficient information.

Because of the overlap between disturbance regimes, with most morphospecies characterising more than one disturbance regime in at least one river, the Indicator Value method was used to identify any individual morphospecies that could act as an indicator or detector species. *P. bellum* and *A. harrisoni* consistently gave high indicator values (> 50%) in natural sites, thus being suitable as detector species (Table 21). In March only, *L. penicillata* gave very high indicator values for natural sites in both rivers, particularly in the Rondegat River where it has potential as an indicator species. No morphospecies gave consistently high indicator values in cleared and alien sites, although *Paragomphus* sp. and *Orthetrum* sp. gave high indicator values for cleared sites and *E. elegans* for alien sites in the Rondegat River. In the Molenaars River, *Athripsodes bergensis* gave high values in alien sites during January.

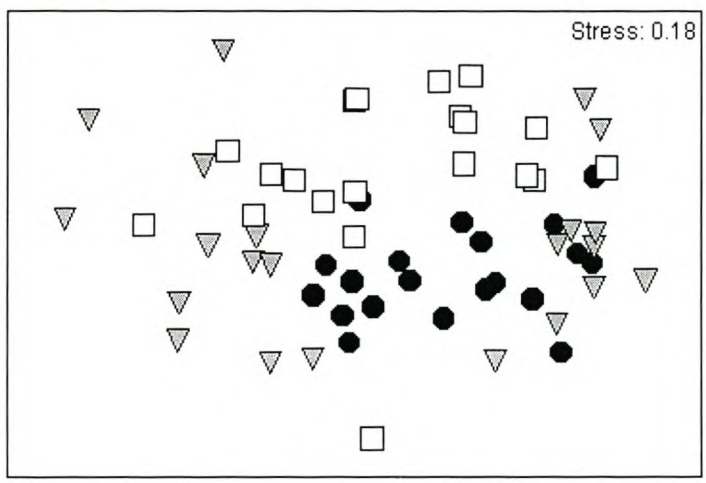
Because *A. penicillata* and *A. harrisoni* are the only morphospecies within the teloganodids and heptageniids respectively, family level identification would probably suffice. However, analysis at morphospecies level did add useful information that resolved patterns within the Baetidae, specifically with regard to identifying *B. harrisoni* and *P. bellum* as potential detector species.

To determine whether morphospecies-level data further elucidated invertebrate-environment relations, a CCA was performed. Again, 'river' and 'month' were the most important variables (eigenvalues of 0.06). Therefore, CCA was performed with these variables partialled out as covariables, thus negating seasonal and between-river effects. The Monte Carlo test confirmed

A. River system



B. Alien disturbance regime



C. vegetation type

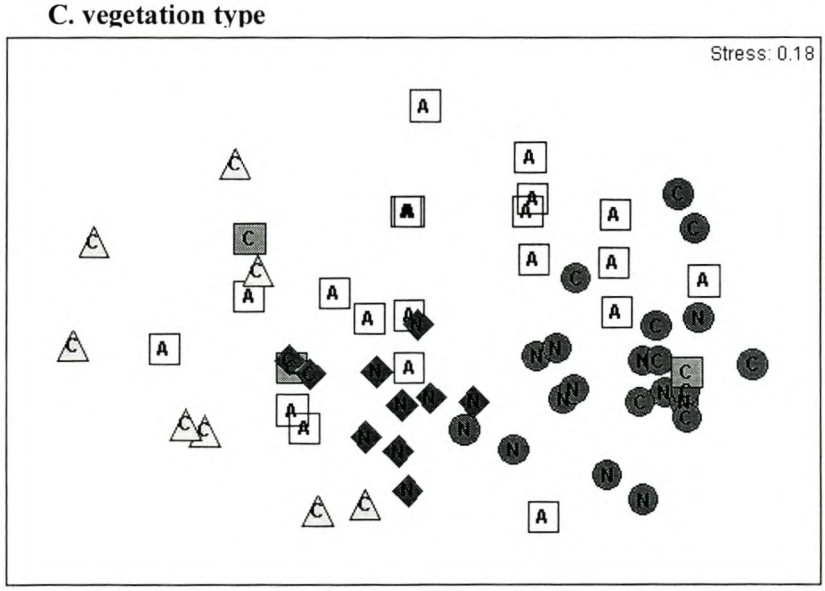


Fig. 11. MDS ordination diagrams of morphospecies abundance data across sites, grouped according to river (A), disturbance regime (B) and dominant vegetation type (C). M = Molenaars River, R = Rondegat River N = natural, C = cleared, A = alien.

Table 18

Morphospecies responsible for differences in abundance patterns between rivers, based on SIMPER analysis of fourth-root transformed abundance data obtained during January and March. Only morphospecies that cumulatively contribute up to 50% of the difference are given.

Morphospecies	Molenaars (mean abundance)	Rondegat (mean abundance)	Average dissimilarity/SD	Contribution to dissimilarity (%)
Lestagella penicillata	177.60	1.31	1.20	7.06
Adenophlebia spp.	19.37	0.38	1.96	5.47
Euthraulus elegans	36.90	2.19	1.60	4.99
Demorepus capensis	15.90	0.69	1.62	4.94
Baetis harrisoni	149.70	17.19	1.49	4.52
Caenis capensis	5.17	14.53	1.69	4.37
Athripsodes bergensis C	11.50	0.69	1.79	4.33
Pseudocloeon bellum	26.50	5.53	1.39	4.19
Paragomphus sp.	0.83	6.84	1.41	3.56
Chloroterpes elegans	4.87	0.63	1.48	3.49

Table 19

Morphospecies responsible for differences in abundance patterns between months, based on SIMPER analysis of fourth-root transformed abundance data collected from both rivers.

Morphospecies	January (mean abundance)	March (mean abundance)	Average dissimilarity/SD	Contribution to dissimilarity (%)
Lestagella penicillata	1.13	166.75	1.22	7.70
Euthraulus elegans	6.83	30.38	1.46	5.10
Pseudocloeon bellum	9.40	21.56	1.36	4.51
Baetis harrisoni	30.97	128.50	1.33	4.41
Adenophlebia spp.	7.13	11.84	1.22	4.20
Caenis capensis	7.57	12.28	1.31	4.06
Demorepus capensis	6.90	9.13	1.21	4.05
Athripsodes bergensis C	2.90	8.75	1.32	3.71
Afronurus harrisoni	16.90	45.25	1.37	3.41
Paragomphus sp.	3.40	4.44	1.19	3.36
Baetidae E	1.63	4.69	1.22	3.31

Table 20

Morphospecies that characterised natural, cleared and alien sites in the Molenaars and Rondegat Rivers during January and March. Only morphospecies contributing up to 70% of the total abundance are mentioned. Percentage contributions are given in brackets. Morphospecies that are consistently characteristic across months and rivers are in bold.

	Overall	Molenaars		Rondegat	
		January	March	January	March
Natural	***Baetis harrisoni* (13.99)** ***Afronurus harrisoni* (12.84)** **Baetidae C (8.44)** *Cheumatopsyche* sp. (8.42) ***Pseudocloeon bellum* (8.37)** *Aeshna* sp. (6.92) Baetidae E (6.49) *Caenis capensis* (4.63)	***Baetis harrisoni* (12.61)** ***Afronurus harrisni* (10.31)** *Adenophlebia* spp. (8.35) **Baetidae C (7.39)** ***Pseudocloeon bellum* (7.06)** *Aeshna* sp. (6.45) *Chloroterpes elegans* (5.88) Baetidae E (5.69)	*Lestagella penicillata* (18.50) ***Baetis* harrisoni (12.30)** ***Afronurus harrisoni* (12.21)** **Baetidae C (6.98)** *Athripsodes bergensis* C (6.81) ***Pseudocloeon bellum* (6.25)** *Cheumatopsyche* sp. (6.19) *Aeshna* sp. (5.62)	*Cheumatopsyche* sp (12.62) ***Baetis harrisoni* (12.28)** ***Afronurus harrisoni* (11.83)** *Caenis capensis* (9.85) *Paragomphus* sp. (7.67) **Baetidae C (6.93)** *Athripsodes* sp. C (6.65) ***Pseudocloeon bellum* (6.47)**	***Baetis harrisoni* (12.54)** ***Afronurus harrisoni* (11.06)** *Caenis capensis* (10.06) ***Pseudocloeon bellum* (9.39)** *Cheumatopsyche* sp (7.39) *Lestagella penicillata* (7.94) **Baetidae C (7.77)** *Aeshna* sp. (7.55)
Cleared	***Baetis harrisoni* (14.20)** *Cheumatopsyche* sp. (12.40) ***Afronurus harrisoni* (11.92)** *Paragomphus* sp. (6.47) Baetidae C (6.25) *Euthraulus elegans* (4.59) *Athripsodes bergensis* C (4.26) *Pseudocloeon bellum* (4.01) *Caenis capensis* (3.85)	***Baetis harrisoni* (9.91)** *Adenophlebia* spp. (9.72) *Demorepus capensus* (9.02) ***Afronurus harrisoni* (7.83)** *Chloroterpes elegans* (7.61) *Cheumatopsyche* sp. (7.20) *Athripsodes bergensis* C (6.12) *Leptophlebiidae* spp. (5.95)	***Baetis harrisoni* (13.73)** *Lestagella penicillata* (11.90) *Euthraulus elegans* (9.15) *Pseudocloeon bellum* (8.63) *Demorepus capensus* (7.68) *Adenophlebia* spp. (7.23) *Athripsodes bergensis* C (6.71) ***Afronurus harrisoni* (5.42)**	*Cheumatopsyche* sp (21.13) ***Afronurus harrisoni* (16.20)** *Paragomphus* sp. (14.91) ***Baetis harrisoni* (13.64)** Baetidae C (6.65)	***Baetis harrisoni* (11.64)** *Cheumatopsyche* sp (10.44) *Caenis capensis* (10.37) ***Afronurus harrisoni* (9.72)** *Paragomphus* sp. (7.96) *Acanthiops* sp. (6.27) Baetidae C (6.26) *Orthetrum* sp. (5.96)
Alien	***Baetis harrisoni* (13.77)** ***Cheumatopsyche* sp. (13.11)** ***Afronurus harrisoni* (12.76)** *Euthraulus elegans* (8.73) *Caenis capensis* (7.33) *Aeshna* sp. (5.72) Baetidae C (5.60) *Athripsodes bergensis* C (3.97) *Adenophlebia* spp. (3.46)	***Cheumatopsyche* sp. (12.85)** ***Baetis harrisoni* (12.06)** *Athripsodes bergensis* C (9.75) *Athripsodes* C (7.26) *Aeshna* sp. (6.20) *Chloroterpes elegans* (6.05) *Pseudocloeon bellum* (5.23) ***Afronurus harrisoni* (4.95)** *Athripsodes bergensis* A (4.57)	***Baetis harrisoni* (11.95)** *Euthraulus elegans* (11.38) *Adenophlebia* spp. (9.66) ***Afronurus harrisoni* (8.52)** *Athripsodes bergensis* C (7.73) *Lestagella penicillata* (7.44) ***Cheumatopsyche* sp (6.81)** *Aeshna* sp. (6.16)	***Afronurus harrisoni* (17.16)** ***Cheumatopsyche* sp. (14.16)** ***Baetis harrisoni* (12.65)** *Euthraulus elegans* (12.28) *Caenis capensis* (11.88) *Aeshna* sp. (7.63)	***Afronurus harrisoni* (16.16)** *Caenis capensis* (14.49) ***Baetis harrisoni* (12.79)** ***Cheumatopsyche* sp. (11.37)** *Euthraulus elegans* (10.61)

Table 21

Potential indicator and detector morphospecies as indicated by their indicator values (in brackets) in alien, cleared and natural sites during January and March in the Molenaars and Rondegat Rivers. Morphospecies with indicator values that are consistently high across rivers and months are in bold.

	Overall	Molenaars River		Rondegat River	
		January	March	January	March
Natural	***Pseudocloeon bellum* (56.01)** ***Afronurus harrisoni* (55.74)** Baetidae C (54.92) Baetidae E (51.09) *Aeshna* sp. (42.57)	***Afronurus harrisoni* (67.36)** Baetidae C (67.34) *Baetis harrisoni* (64.93) *Pseudagrion* A (60.95) *Hydroptila capensis* (60.00) ***Pseudocloeon bellum* (48.51)**	*Lestagella penicillata* (64.12) Baetidae C (57.05) ***Afronurus harrisoni* (56.83)** ***Pseudocloeon bellum* (54.19)** *Aeshna* sp. (45.52%)	*Athripsodes* C (66.10) *Baetis harrisoni* (64.24) Baetidae E (62.77) *Caenis capensis* (62.49) ***Pseudocloeon bellum* (59.87)** *Cheumatopsyche* sp. (56.12) ***Afronurus harrisoni* (50.15)**	*Lestagella penicillata* (93.23) ***Pseudocloeon bellum* (92.62)** *Baetis harrisoni* (71.65) Baetidae E (63.64) Baetidae C (58.82) *Caenis capensis* (53.28) ***Afronurus harrisoni* (52.46)**
Cleared	*Baetis harrisoni* (53.65)	*Baetis harrisoni* (54.25) *Pseudagrion* B (46.30) *Chloroterpes elegans* (45.76)	*Baetis harrisoni* (67.42) *Demorepus capensus* (53.55) *Athripsodes bergensis* C (49.06)	*Paragomphus* sp. (50.10) *Orthetrum* sp. (42.61)	*Orthetrum* sp. (75.14) *Leptecho helicotheca* (54.35) *Paragomphus* sp. (51.13) *Trithemis* A (47.41)
Alien	*Caenis capensis* (35.03) *Cheumatopsyche* sp. (34.90)	*Athripsodes bergensis* A (69.19) *Cheumatopsyche* (63.37) *Athripsodes bergensis* C (52.57) *Athripsodes bergensis* B (51.43) *Athripsodes* C (47.46)	Baetidae A (51.79) *Zygonyx natalensis* (48.46)	*Euthraulus elegans* (86.60) *Acanthiops* sp. (49.35)	*Euthraulus elegans* (78.87) *Cheumatopsyche* (46.11)

that the measured environmental variables accounted for a significant amount of variation of the first axis (F = 4.109, P = 0.004) and the overall ordination (F = 1.702, P = 0.002). The species-environment correlation was strong (greater than 0.80 on all axes) and the environmental variables were responsible for the main variation in invertebrate distribution patterns (cumulative percentage variance of invertebrate data and invertebrate-environment relations = 58.9%). The total inertia was 0.1. Bank exposure was strongly correlated with axis 1, while dissolved oxygen and *Prionium* were strongly correlated with the second axis.

The Monte Carlo test of variables considered individually (marginal effects) confirmed the family-level finding that bank exposure, disturbance regime, indigenous bushes, *Prionium*, width, alien trees and dissolved oxygen were the most important variables (Table 22). Bank exposure was elevated in importance and was now the most important variable. In addition, sedge (which included grass) was also important at the morphospecies level, having a significant effect on abundance patterns when considered collectively (conditional effects). A comparison of the CCA ordination diagrams based on family-level abundances (Fig. 7) and morphospecies abundances (Fig. 12) shows the arrows to be, not only of similar lengths, but also similarly arranged with respect to the axes and the sites. However, the morphospecies level provided greater statistical power to detect important environmental variables.

L. penicillata, *P. bellum*, *A. harrisoni*, baetid E, *Anax* sp., *P. bellum* and *Pseudagrion* A were associated mainly with natural sites (Fig. 13). Baetid C was associated mainly with cleared sites but its positions near the origin indicated overlap between disturbance regimes. *Paragomphus* sp., *Ecnomus* sp., *Orthetrum* sp., *Trithemis* A and B, *Hydroptila capensis* and *Pseudagrion* B were associated most strongly with cleared sites, while *E. elegans* and *Adenophlebia* sp. were associated mainly with alien sites.

With the exception of *Aeshna* sp. and *Zygonyx* sp., all Odonata species were associated with natural and cleared sites with an abundance of marginal vegetation that included indigenous bushes, grass and sedge and *Prionium* (Fig. 14). These included *Pseudagrion* A and B, *Trithemis* A and B, *Anax* sp. and *Paragomphus* sp. *Anax* sp. and *Pseudagrion* A were associated mainly with natural sites, while *Trithemis*, *Pseudagrion* B and *Paragomphus* sp. were associated mainly with cleared sites with higher temperatures and an availability of pool biotopes. The ephemeropteran, *P. bellum*, and the trichopteran, *Hydroptila*, were also associated with these conditions, the latter species occurring mainly in warm cleared sites and the former species in wide natural sites. *L. penicillata* occurred mainly in wide, deep natural sites with relatively strong flow rates and an abundance of indigenous bushes and sedges. *A. harrisoni* was associated mainly with strong flow conditions, which mostly occurred in natural and dense alien sites. *E. elegans*, *Aeshna* sp., *Cheumatopsyche* sp. and *Adenophlebia* sp. were associated with high flow rates and alien trees, while *A. bergensis* B and C and *Zygonyx* sp. were associated mostly with exposed banks, alien trees and sand and gravel substrates, in both cleared and alien sites.

The clear association of several morphospecies with marginal vegetation prompted a SIMPER analysis of distribution patterns across dominant vegetation types. The Odonata were the only morphospecies to give characteristic assemblages that did not overlap across all three disturbance regimes (Table 23). *Pseudagrion* A characterised sites with an abundance of indigenous vegetation and *Prionium*, while *Aeshna* sp. characterised sites with trees, whether alien or indigenous. *Pseudagrion* B characterised sites with high levels of *Prionium* and *Orthetrum* sp. characterised grassy sites. *Paragomphus* sp. and *Trithemis* A were common in sites with an abundance of grass, sedge and *Prionium*.

CCA performed on each disturbance regime in each river showed that different environmental variables were important in each river (Table 24). Only suspended solids and percentage gravel were consistently important in cleared sites. Relatively few variables were important in natural

Table 22

Environmental variables, in descending order of importance in affecting morphospecies abundance patterns, as indicated by their eigenvalues. The geographical and seasonal effects were partialled out by taking the variables 'river' and 'month' as covariables. *P* = significance level of the fit as obtained from the Monte Carlo Permutation test with each variable considered individually (marginal effects) and collectively by forward selection (conditional effects). Canopy cover and percentage alien trees were strongly co-correlated and therefore considered as a single variable.

	Marginal effects			**Conditional effects (Forward selection)**	
	Eigenvalues	***P***		**Eigenvalues**	***P***
Bank exposure (%)	0.06	0.002	Bank exposure (%)	0.06	0.002
Disturbance regime	0.06	0.002	Dissolved oxygen	0.06	0.002
Indigenous bushes (%)	0.06	0.002	*Prionium* (%)	0.04	0.002
Prionium (%)	0.06	0.002	Width	0.03	0.006
Width	0.06	0.002	Alien/ canopy cover	0.02	0.028
Alien/ canopy cover (%)	0.05	0.002	Sedge/grass (%)	0.02	0.018
Dissolved oxygen	0.05	0.002	Indigenous bushes (%)	0.02	0.026
Sedge/grass (%)	0.05	0.002			
Flow	0.04	0.062			
Depth	0.03	0.028			
Sand (%)	0.03	> 0.05			
Pool (%)	0.03	> 0.05			
Gravel (%)	0.03	> 0.05			
Temperature	0.02	> 0.05			
Conductivity	0.02	> 0.05			
Cobbles (%)	0.02	> 0.05			
Eucalyptus (%)	0.02	> 0.05			
TSS	0.02	> 0.05			
pH	0.02	> 0.05			
Riffle (%)	0.01	> 0.05			

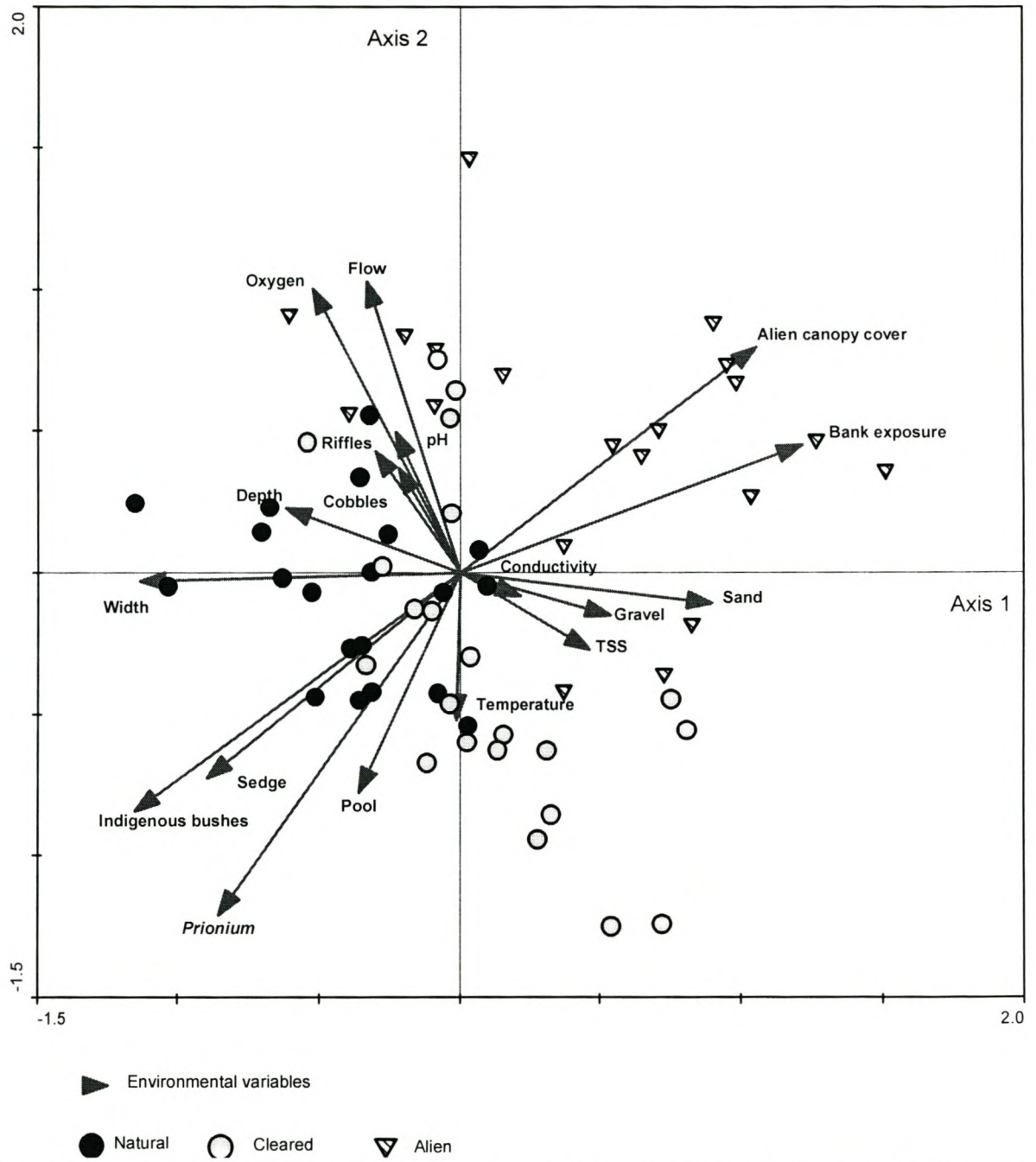


Fig. 12. CCA ordination diagram of sites and environmental variables affecting morphospecies distribution patterns across disturbance regimes in the two rivers. The variance accounted for by the first two axes was 54.1%. Eigenvalues were 0.092 and 0.073 on axes 1 and 2 respectively.

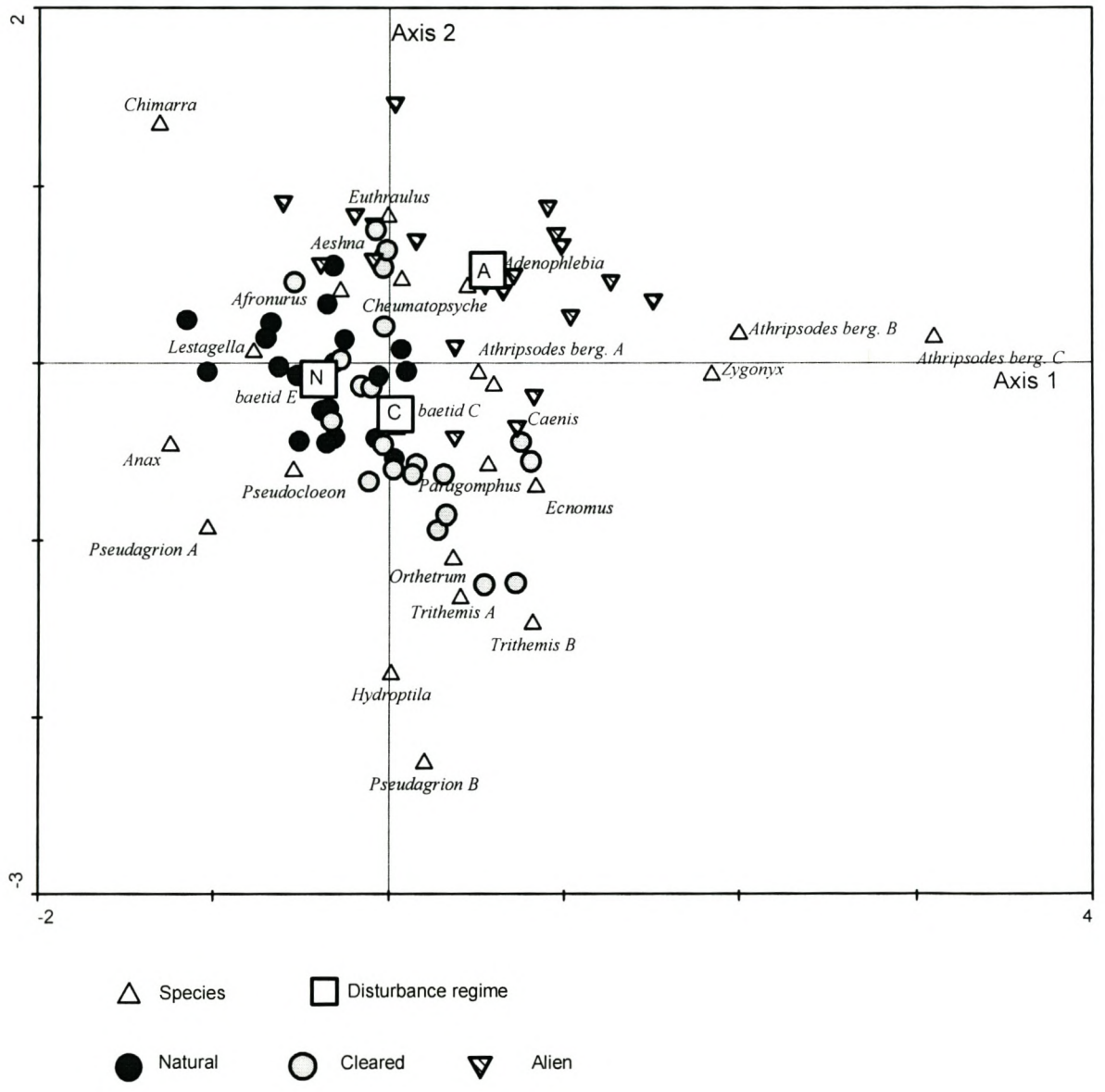


Fig. 13. CCA ordination diagram of morphospecies abundance patterns across sites. Disturbance regimes are represented as centroids of the sites. (N = natural, C = cleared and A = alien).

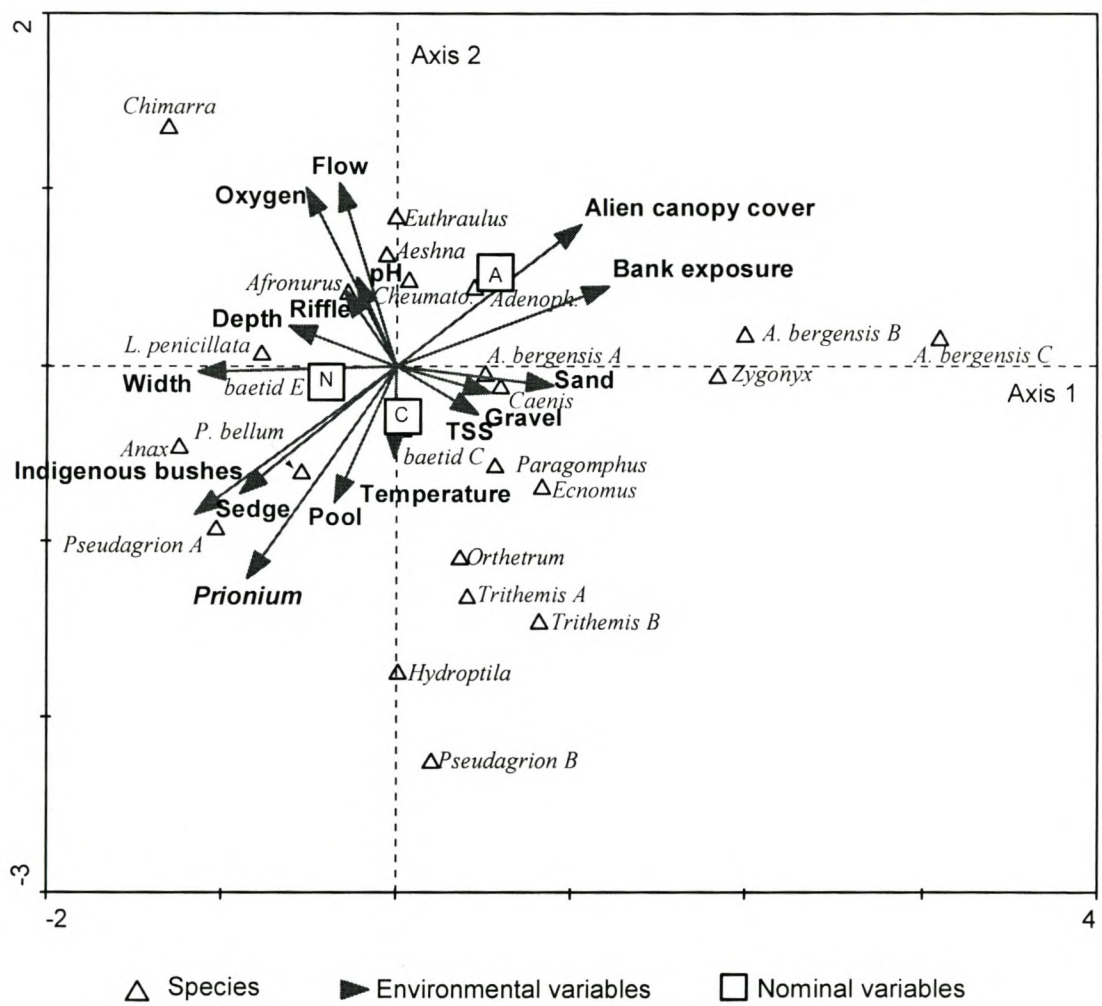


Fig. 14. CCA ordination diagram of environmental variables affecting the distribution patterns of the most common morphospecies across sites. Sites within each disturbance regime are represented as centroids (N = natural, C = cleared and A = alien).

Table 23

SIMPER analysis of Odonata morphospecies.

Dominant vegetation type	Characteristic morphospecies	Percentage contribution
Indigenous trees/bushes		
	Aeshna	64.37
	Paragomphus	18.59
	Pseudagrion A	12.03
Prionium		
	Paragomphus	60.51
	Pseudagrion B	10.42
	Pseudagrion A	8.85
	Trithemis A	6.48
Grass and sedge		
	Paragomphus	66.89
	Orthetrum	27.36
	Trithemis A	13.39
Alien *Acacia*		
	Aeshna	67.49
	Paragomphus	27.23

Table 24

Environmental variables affecting morphospecies distribution patterns in each disturbance regime and in each river. Month and river were partialled out as covariables. CCA results were statistically tested using the Monte Carlo permutation test and only significant results are shown (with the significance level given in brackets).

	Overall	**Molenaars River**	**Rondegat River**
Natural	Oxygen (0.05) pH (0.05)	pH (0.05)	Cobbles (0.05)
Cleared	Indigenous bushes (0.01) *Prionium* (0.01) Oxygen (0.01) Sand (0.02) Width (0.04) pH (0.04)	Gravel (0.01) Width (0.03) Sand (0.03) *Prionium* (0.04) Suspended solids (0.04) pH (0.05)	Indigenous bushes (0.002) Suspended solids (0.01) Gravel (0.01) Grass and sedge (0.01) Temperature (0.01) Oxygen (0.01)
Alien	Temperature (0.02) *Prionium* (0.03) Bank exposure (0.04)	Pools (0.02) Bank exposure (0.04)	*Prionium* (0.004)

and alien sites, compared to a wide range of variables in cleared sites. This indicates that cleared sites varied greatly in environmental conditions and invertebrates therefore showed highly variable responses in these sites.

3.7. Multivariate analysis of SASS presence/absence data

CLUSTER analysis of presence/absence of SASS taxa again indicated an overriding between-river effect with no clear grouping according to disturbance regime or month (Fig. 15). ANOSIM gave a significant difference between rivers ($R = 0.55$, $P = 0.1\%$) but, at this level, there was no significant difference between months (revealed $R = 0.052$, $P = 2.6\%$). While there was no overall significant difference between disturbance regimes ($R = 0.072$, $P = 0.3\%$), a significant difference was detected between natural and alien sites ($R = 0.149$, $P = 0.2\%$), but not between cleared and natural ($R = 0.035$, $P = 12.8\%$) or between cleared and alien sites ($R = 0.044$, $P = 8.5\%$). This result was consistent for both rivers when analysed individually.

Natural sites were consistently characterised by Leptoceridae, Aeshnidae, Baetidae and Heptageniidae, and alien sites by Baetidae and Hydropsychidae, although their percentage contributions were not consistent across rivers (Table 25). With the exception of Corydalidae, all taxa characterised more than one disturbance regime in at least one river. Corydalidae, together with Heptageniidae, characterised natural sites only, but this was not consistent across rivers, as they only characterised Molenaars River natural sites. Similarly, Helodidae and Aeshnidae characterised natural sites only, but only in the Rondegat River, while libellulids characterised cleared sites along the Rondegat River only. Taxa that were most responsible for the significant difference between natural and alien sites included Coenagrionidae and Teloganodidae (10% contribution). However, only Teloganodidae was responsible for differences in both rivers, Coenagrionidae being responsible for differences in the Molenaars River only.

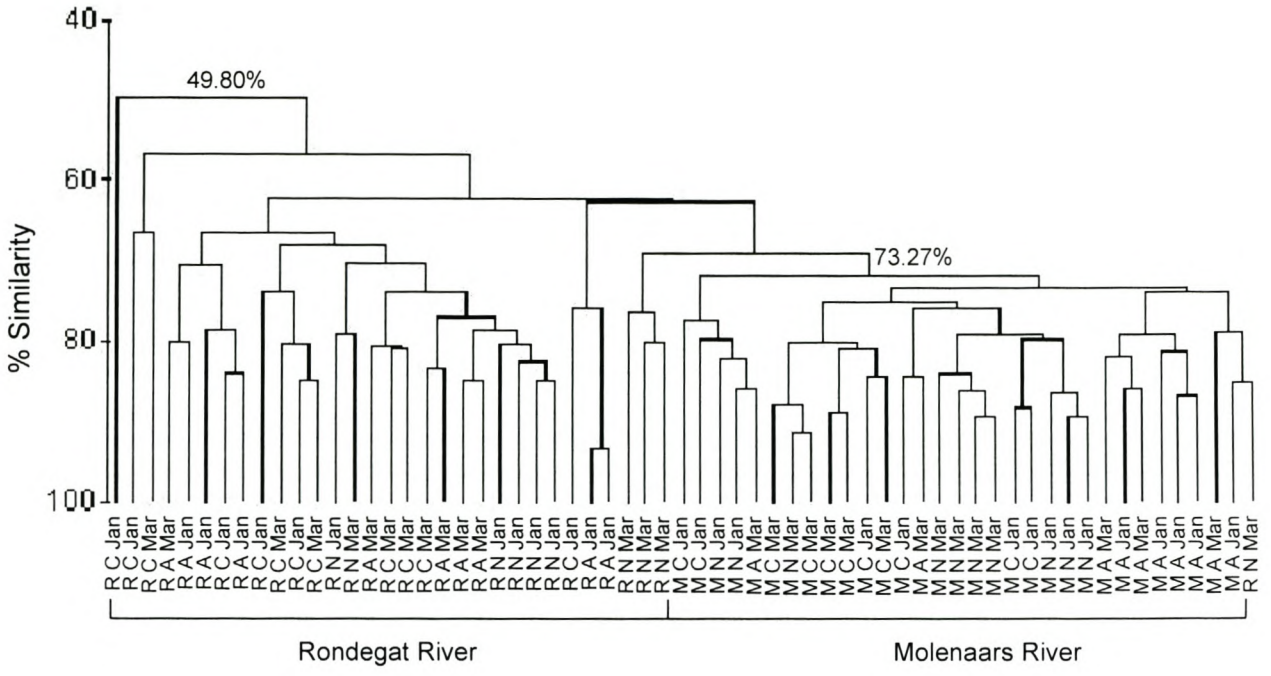


Fig. 15. CLUSTER dendrogram of sites based on SASS taxon presence/absences in alien (A) cleared (C) and natural (N) sites in the Molenaars (M) and Rondegat (R) Rivers during January (Jan) and March (Mar).

Table 25

SASS taxa that characterise natural, cleared and alien sites along the Molenaars and Rondegat Rivers, based on SIMPER analysis of presence/absence data. Only taxa cumulatively contributing up to 70% of the total abundance are indicated.

	Overall	**Molenaars River**	**Rondegat River**
Natural	*Leptoceridae (7.28%)*	Leptoceridae (6.90%)	Leptoceridae (6.82%)
	Aeshnidae (7.28%)	Aeshnidae (6.90%)	Aeshnidae (6.82%)
	Baetidae (7.28%)	Simuliidae (6.90%)	Baetidae (6.82%)
	Heptageniidae (7.28%)	Baetidae (6.90%)	Heptageniidae (6.82%)
	Elmidae (7.28%)	Heptageniidae (6.90%)	Caenidae (6.82%)
	Hydropsychidae (6.55%)	Elmidae (6.90%)	Hydropsychidae (6.82%)
	Chironomidae (6.55%)	Athericidae (6.90%)	Elmidae (6.82%)
	Simuliidae (5.94%)	Oligochaeta (6.90%)	Chironomidae (6.82%)
	Corydalidae (5.89%)	Corydalidae (6.90%)	Veliidae (6.82%)
	Helodidae (5.78%)	Helodidae(5.58%)	Gomphidae (5.26%)
	Athericidae (5.78%)	Hydropsychidae (5.54%)	Helodidae (5.26%)
Cleared	*Baetidae (9.54%)*	Leptoceridae (7.42%)	Baetidae (9.91%)
	Hydropsychidae (8.74%)	Simuliidae (7.42 %)	Heptageniidae (9.91%)
	Elmidae (8.44%)	Baetidae (7.42 %)	Hydropsychidae (9.91%)
	Chironomidae (7.85%)	Leptophlebiidae (7.42 %)	Gomphidae (8.31%)
	Heptageniidae (6.28%)	Elmidae (7.42 %)	Libellulidae (8.16%)
	Simuliidae (6.12%)	Chironomidae (7.42 %)	Elmidae (7.79%)
	Leptoceridae (5.17%)	Aeshnidae (6.19%)	Chironomidae (7.79%)
	Aeshnidae (4.65%)	Teloganodidae (6.07%)	Caenidae (6.37%)
	Gomphidae (4.65%)	Hydropsychidae (6.07%)	Veliidae (4.73%)
	Veliidae (4.64%)	Helodidae (5.96%)	
	Libellulidae (4.51%)		
Alien	*Baetidae (8.60%)*	Leptoceridae (6.66%)	Baetidae (9.39%)
	Hydropsychidae (8.60%)	Simuliidae (6.66%)	Heptageniidae (9.39%)
	Elmidae (8.60%)	Baetidae (6.66%)	Caenidae (9.39%)
	Chironomidae (8.60%)	Leptophlebiidae (6.66%)	Hydropsychidae (9.39%)
	Heptageniidae (7.63%)	Hydropsychidae (6.66%)	Elmidae (9.39%)
	Leptoceridae (7.53%)	Elmidae (6.66%)	Chironomidae (9.39%)
	Caenidae (5.51%)	Helodidae (6.66%)	Veliidae (7.49%)
	Veliidae (5.47%)	Athericidae (6.66%)	Leptoceridae (7.18%)
	Simuliidae (5.15%)	Chironomidae (6.66%)	

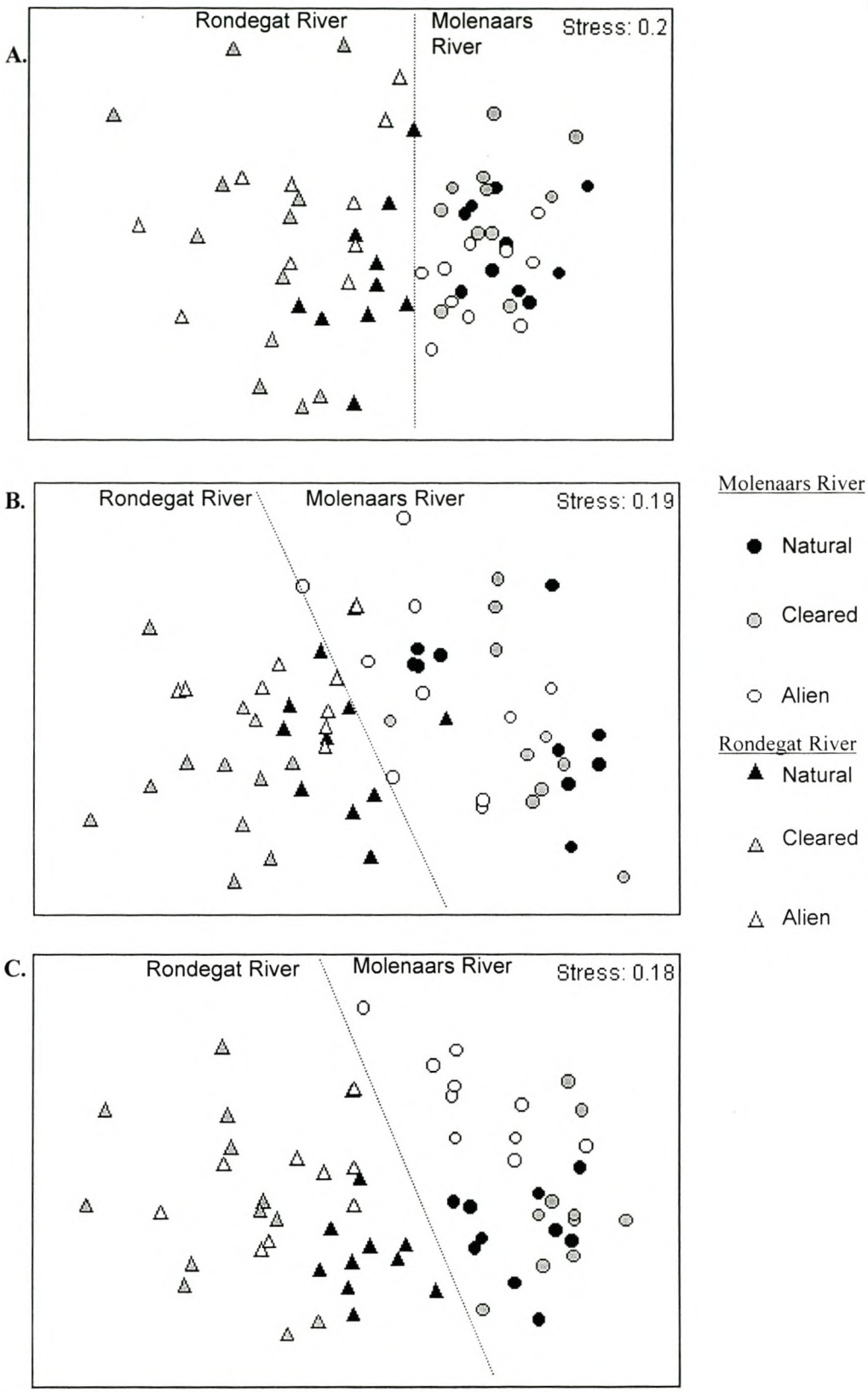


Fig. 16. MDS diagrams of sites based on: (A) family-level presence/absence data (all SASS families), (B) family-level abundance data (EPT+O) and (C) morphospecies abundance (EPT+O). Circles indicate Molenaars River sites and triangles indicate Rondegat River sites.

Fig. 16 compares the site groupings given at increasing levels of taxonomic resolution. Morphospecies abundance data showed the clearest grouping according to both disturbance regime and river system, with an overall significant difference between disturbance regimes (ANOSIM; $R = 0.61$, $P = 0.1\%$). In fact, at this level, only natural and cleared sites along the Molenaars River were not significantly different. Neither family-level nor presence/absence data gave overall significant differences between disturbance regimes. Both these levels gave significant differences between natural and alien sites ($R > 0.149$, $P < 0.2\%$) but only the family-level data also gave a significant difference between cleared and alien sites ($R < 0.09$, $P > 1\%$).

4. Discussion

King and Schael (2001) found that, in the Western Cape, each river and catchment has its own signature, in terms of its benthic macroinvertebrate fauna. This is the result of a long period of geological and climatic stability and the isolation of individual catchments, resulting in a unique assemblage of aquatic organisms (Wishart *et al.*, 2003). In particular, species with limited dispersal abilities (e.g. Plecoptera) have shown species and genetic differences between catchments (Wishart *et al.*, 2003). These signiature differences result in each river functioning in its own unique way and therefore responding to disturbance in different ways. The result is that ecological data obtained from one river cannot necessarily be extrapolated to another. This study confirmed that each river responded differently to disturbance by alien invasion and clearing, making it difficult to make generalisations. As a result, each river had to be assessed individually to seek common trends.

4.1. Environmental responses to alien disturbance

Water quality variables that have been found to change as a result of removing riparian vegetation have included temperature, light, fine sediments, salinity (measured as conductivity in this study), pH, dissolved oxygen, habitat quality and availability, allochthonous input of organic plant debris,

shading and bank stability (King *et al.*, 2003; Uys, 2003). In this study, removal of alien *Acacia* trees resulted in greater exposure of the river and riverbanks to sunlight, thus encouraging the growth of marginal grass, sedge and *Prionium*. It also resulted in reduced shading of the river, so that water temperatures in cleared sites were higher than in natural sites, a particular concern in Western Cape rivers as most endemic species are adapted to cold water conditions. Certain taxa, such as adult notonemourids, are also adapted to humid conditions with total canopy cover, thus not being unduly affected by alien trees, but undoubtedly being harmed by a sudden and complete removal of these trees (Wishart *et al.*, 2003). In addition, reduced plant cover may make invertebrates more vulnerable to inclement weather (e.g. heat, wind) or to predators (Stubbs and Warren, 1991), as refuge areas are removed. Invertebrates are also likely to be exposed to far greater diurnal and seasonal fluctuation in factors such as temperature, sunlight, turbidity and oxygen.

The higher temperatures in cleared sites may also have had other less obvious affects, such as earlier emergence times, increased metabolism and growth and increased bioavailability of nutrients (Malan and Day, 2002), while low temperatures in alien sites may have had the opposite effects.

The low oxygen levels in cleared sites were probably due to the higher water temperatures, as increased temperatures reduce the solubility of oxygen (Dallas *et al.*, 1994). CCA established that, of all the water quality variables measured, only oxygen had an important influence on invertebrate distribution patterns. Low oxygen levels impact upon emergence, reproduction, growth rate and food intake (King *et al.*, 2003), while increased temperatures also influence that rate of decomposition of organic matter (Stubbs and Warren, 1991). In contrast to cleared sites, alien sites had the lowest temperatures with relatively high oxygen levels.

Also associated with cleared sites were sand and gravel substrate, high levels of suspended solids and high conductivity. This is cause for concern as it points to erosion of exposed (cleared) banks. Deforestation or clearing of river banks is regularly associated with increased erosion and fine sediments (Maridet *et al.*, 1996; Uys, 2003; Vuori and Joensuu, 1996) and bank instability resulting from vegetation clearing is one of the major stream degradation issues in Australia (Rutherfurd *et al.*, 2000a, b). The impact on benthic invertebrates is dependent on both the amount and type of sediment entering the stream (Vuori and Joensuu, 1996). High suspended solids levels can affect other water quality variables (e.g. temperature, light, turbidity), nutrient levels, the availability of habitats (e.g. smothering of habitat or food) and the well-being of aquatic species (e.g. reduced feeding efficiency and growth rate) (Rutherfurd *et al.*, 2000a). Suspended solids may, for example, clogg the gills of filter-feeders or settle on rocky substrates, thus reducing habitat availability (Malan and Day, 2002). High levels are usually accompanied by low densities of benthic organisms and a reduction in species biodiversity (Dallas and Day, 1993; King *et al.*, 2003; Rutherfurd *et al.*, 2000a).

Cleared sites are more exposed, not only to sunlight, but also to wind. Wind-blown debris may have contributed to the high concentrations of suspended solids. Cleared areas are also generally burnt after alien trees have been removed. This may exacerbate erosion and increase concentrations of suspended solids from dust or ash, as has been found with wildfires in afforested catchments (Scott *et al.*, 1998). The effects of fires on soils and water quality depend on the intensity of the fire and the presence of riparian vegetation (Scott *et al.*, 1998). Alien trees burn at higher intensities and the lack of indigenous riparian vegetation in cleared areas makes fire disturbance a greater risk. The high intensity of fires may damage soils, which may compromise the ability of indigenous vegetation to recover and can result in water repellency and increased erosion (Scott, *et al.*, 1998). Fires have also been found to destroy indigenous seed

banks (Richardson and van Wilgen, 1986; Holmes *et al.*, 2000) and to volatise nutrients, thus increasing levels of dissolved solutes (Scott, *et al.*, 1998).

Cleared sites had the greatest prevalence of sand and gravel substrates, a likely result of increased erosion. Substrate composition has been found to be an important determinant of invertebrate distributions (Wright *et al.*, 1984) and, in this study, sand and gravel substrates were found to influence assemblage patterns in cleared sites. For example, the high number of gomphids in cleared sites may merely be a response to the availability of sandy substrates, their preferred habitats (Corbet, 1999). In addition to physical disturbance of habitats, sand can also restrict the ability of many riffle insects to move on the substrate (Luedtke and Brusven, 1976) and the movement of sand particles could induce physical stress (Vuori and Joensuu, 1996).

Sandy substrates, together with high levels of suspended solids, were also associated with alien sites, this as a result of erosion of the highly exposed banks that lacked the stabilising effect of marginal vegetation. Pienaar *et al.* (2004, unpublished report) similarly found soil under alien trees to have higher ratios of course sand than under indigenous riparian trees. They concluded that the soil is modified by alien trees and becomes unsuitable for the recovery of indigenous vegetation after alien clearing, so that active management (e.g. flushing of sediments and cultivation) is required.

It is clear, therefore, that alien disturbance affected, not only water quality (e.g. temperature, oxygen and suspended solids), but also aquatic habitats (e.g. marginal vegetation and substrate composition).

4.2. Water quality effects (SASS)

Alien disturbance does not appear to unduly affect water quality as measured by SASS, as overall differences between disturbance regimes were not statistically significant. However, SASS scores

were, on average, highest in natural sites and relatively low in alien and cleared sites, suggesting little improvement in water quality conditions after alien clearing.

Where low SASS scores were given for alien sites, this was as a result of low incidences of sensitive taxa, such as teloganodids, sericostomatids, athericids, helodids, corydalids and aeshnids. These taxa are clearly less tolerant of shaded alien-affected conditions. ASPT scores were relatively high for alien sites, indicating that, where sensitive taxa are lost, they are not replaced by more tolerant taxa. In fact, the incidence of tolerant taxa was lowest in alien sites.

Cleared sites had scores that matched or were lower than alien scores, suggesting only marginal improvement in conditions or deteriorating conditions after alien trees were removed. The low incidence of high-scoring taxa in cleared sites suggests a loss of these taxa as a result of impaired water quality conditions, clearly a cause for concern. As oxygen emerged as an important environmental variable, it is likely that the low oxygen concentrations in cleared sites were limiting for these sensitive taxa, resulting in lower SASS scores. High levels of suspended solids and sediment as a result of erosion of cleared banks, may have compounded this effect. Those affected included sericostomatids, helodids, athericids, corydalids and aeshnids. In contrast, these taxa, together with heptageniids, teloganodids and philopotamids, were responsible for the high scores in natural sites.

Alien invasion caused a loss of both sensitive and tolerant taxa. Removal of aliens appeared to cause an even further loss of sensitive taxa, but these were replaced with more tolerant taxa. These tolerant taxa included mostly coenagrionids, libellulids, hydroptilids and naucorids. Corixids, notonectids, gerrids and dytiscids were also favoured by cleared conditions.

Therefore, where recovery had occurred, it was mainly the less sensitive, widespread taxa that had benefited. These included mostly hemipterans and odonates that were probably responding to the increased availability of marginal vegetation in cleared sites. As Usher and Jefferson (1993) point

out, sites restoration will rely largely on natural colonisation by more ubiquitous, eurytopic species. For example, eurytopic, vagile, widespread Odonata have been found to be the first to colonise newly-created biotopes, such as dams (Steytler and Samways, 1995). Temporally varying environments are also thought to favour generalists over specialists in terms of relative fitness (Wilson and Yoshimura, 1994), so that the increased diurnal and seasonal fluctuations in temperature and insolation found in exposed cleared sites, may favour more tolerant generalists. Rare, endemic or stenotopic species may take longer to return after alien clearing and may even have to be translocated from other geographical areas (Samways, 1994).

4.3. Linking SASS to disturbance by aliens

Trends in SASS scores were inconsistent between rivers, making generalisations difficult. Alien sites, in particular, were not consistent. For the most part, alien sites gave the lowest SASS scores in the five Western Cape Rivers sampled. However, in the Molenaars River, SASS and ASPT scores in alien sites were even higher than in natural sites, suggesting that alien conditions may, surprisingly, favour certain sensitive taxa. Similarly, responses to alien clearing were inconsistent. Of the five Western Cape rivers sampled, three rivers had slightly higher scores in cleared sites than in alien sites, suggesting some measure of post-clearing improvement in conditions. However, in the Molenaars River, there was an apparent decline in conditions after alien removal, while in the Rondegat River, there was no marked improvement in conditions after alien clearing.

These inconsistent responses pose the questions: can SASS scores be interpreted solely according to the effects of alien disturbance on water quality, or are other factors involved? It is possible that different rivers, being signiatures, respond differently to alien disturbance? Is it likely that benthic macroinvertebrates were responding to factors other than of alien disturbance? SASS was developed to detect the impairment of water quality. However, factors affecting biotic communities are usually complex and interrelated and the distribution of benthic

macroinvertebrates may be as a result of factors other than water quality (Rosenberg and Resh, 1993). In addition, alien trees and their removal create environmental conditions that are interlinked to a large degree so that it becomes difficult to isolate the effects that are due to alien disturbance. It is therefore difficult to establish whether changes are as a result of disturbance or part of natural fluctuations in the system (Dallas *et al.*, 1994) and careful interpretation is required. Macroinvertebrates may be responding to a variety of factors over an indefinite time period and may not simply be responding to alien disturbance at the time of sampling.

Other factors could include, for example, biotope availability, insolation or flow velocity (Dallas, 1997). Certain taxa exhibit a degree of habitat specificity (Dallas, 2002) so that the number and types of biotopes available, and thus sampled, may affect scores. Moreover, certain biotopes have more sensitive taxa associated with them (e.g. riffles) than others (e.g. marginal vegetation) (Armitage *et al.*, 1983; Dallas, 1997). A limitation of SASS is that it becomes more reliable as the number of available biotopes increases (Uys *et al.*, 1996). In this study, sites that had sand biotopes present were compared with those without, while the type and amount of marginal vegetation also varied considerably between sites. However, all available biotopes were sampled according to the sampling protocol and an attempt was made to minimise these biotope differences. Moreover, IHAS scores were not correlated with SASS or ASPT scores, indicating that biotope availability did not unduly affect results. Nevertheless, time constraints did not allow for separate analysis of each biotope, so that the final results may have reflected biotope differences as well as disturbance differences.

It is also possible that the small sample sizes were not representative of the disturbance regime as a whole. Outlying data points from single exceptional values may have had undue influence on the overall results. King *et al.* (2003), for example, found that disturbed sites showed greater variability, thus requiring greater sampling effort for representative results.

Furthermore, Dallas (1997, 2002) cautions that SASS scores differ longitudinally down a river, so that it becomes difficult to distinguish water quality effects from zonation effects. Moreover, it is the extremes of water quality variation that have the major impacts on faunal composition (Chutter, 1994) and it is possible that alien disturbance, unless extreme, did not necessarily disrupt communities sufficiently to be detected by SASS scores. A final consideration is that sensitivity scores are subjectively assigned and it is unlikely that tolerance levels are consistent across all regions (Phiri, 2000).

In the Rondegat River, cleared and alien scores were far lower than in natural sites, suggesting that secondary factors, unrelated to alien disturbance, may have influenced water quality in these sites. Alien and cleared sites were surrounded by farmland occasionally used for grazing by horses and goats. Trampling and nutrient enrichment due to organic runoff may have influenced the water quality, although this effect would have been spread across all cleared and alien sites, so that any differences between them would have been mainly due to alien disturbance. A second likely explanation is the abundance of *Eucalyptus* trees in Rondegat River cleared and alien sites. (These trees were absent from the Molenaars River.) The polyphenols in *Eucalyptus* leaves reportedly inhibit growth of detritivores and colonisation by shredders (Bunn, 1988; Canhoto and Graca, 1995). In addition, natural sites occurred at a higher altitude than cleared and alien sites and the high scores in natural sites may have been reflecting a SASS score more typical of mountain streams (i.e. over 140) than of foothills (120) (Dallas *et al.*, 1998).

The high SASS scores in Molenaars River alien sites is unexpected and may indicate that not all high-scoring sensitive taxa are sensitive to the disturbance caused by alien trees. These alien sites had dense alien growth and were highly shaded and cooler than other sites. They also had highly cobbled substrates and stronger flow rates, and therefore had higher levels of dissolved oxygen. The presence of these more sensitive taxa may have been a response to any of these conditions. That is, higher oxygen levels in cool, shaded, alien sites may override the negative effects of

invasion (e.g. increased erosion and suspended solid concentrations). In addition, the high availability of plant debris and leaf fragments from *Acacia* trees in these sites may have favoured shredders, such as notonemourids and barbarochthonids.

These taxa may therefore also have been responding to factors unrelated to alien disturbance. For example, notonemourids are known to prefer the fast-flowing riffle and run habitats that dominated in these sites, while the adults are associated with the high humidity of well-canopied rivers (Wishart, *et al.*, 2003). Similarly, scrapers, such as glossosomatids and certain leptophlebiids, are often associated with cobbled substrates (Davies, 1994), so that their presence in these sites may merely have been a response to favourable substrate conditions.

A further consideration is that the high flow rates in these sites possibly resulted in rejuvenation of the river from a foothill to a mountain stream condition, so that SASS scores merely reflected zonation, rather than improved water quality conditions. This would also explain the abundance of notonemourids, which are typically found in mountain streams, in this section of river.

The high incidence of oligochaetes in all Molenaars River sites, particularly in natural sites, suggests that additional disturbances may have affected water quality. Brown (2001) found that effluent from an upstream trout farm affected SASS scores 1 km downstream. The natural sites in this study were approximately 8 km downstream of the trout farm but it is possible that they were still affected. Cleared and alien sites were 1-2 km further downstream and may have been less affected.

These inconsistent and complex responses to alien disturbance suggest, therefore, that, while SASS may provide useful qualitative information on overall river health, it should not be 'over-interpreted' (e.g. identifying cause and effect relationships). That is, care should be taking when attributing SASS scores to 'alien disturbance' alone. Moreover, variable responses to water quality within taxa such as Trichoptera and Ephemeroptera, suggest that multivariate analysis of

abundance data, or identifications at levels lower than family, may be more accurate evaluations of responses to alien disturbance.

4.4. Seasonal effects on water quality and SASS scores

SASS scores were clearly affected by seasonal changes in invertebrate communities. Scores were higher in autumn (March) than summer (January) which agrees with the findings of other authors (Armitage, *et al.*, 1983; Dallas, 1997; Gratwicke, 1998). Gratwicke (1998) attributed the lower summer scores to the concentrating effect of hot, dry weather conditions. Streams in mediterranean climates, such as in the southwestern Cape, are prone to dry, hot conditions in late summer months (i.e. January) that result in a number of stream conditions: increased salinity, increased deposition of sediments, erosion of drying banks and highly fluctuating oxygen levels (Dallas *et al.*, 1998). Oxygen fluctuations are caused by a combination of factors: higher temperatures, high daytime photosynthesis and night-time respiration, higher oxygen demand due to increased algal production, reduced dilution of chemicals and reduced turbulence (Dallas *et al.*, 1998; Gasith and Resh, 1998).

The higher scores in March were, however, only evident in cleared and alien sites. Gratwicke (1998) similarly found that seasonal differences were greater in polluted sites along a river in Zimbabwe. Weatherley *et al.* (1989) attributed this phenomenon to the low faunal density and diversity in disturbed sites, this resulting in the low occurrence of invertebrates at certain times. This is a likely explanation for the greater seasonal changes evident in cleared and alien sites, which also had lower abundances and diversities.

However, despite seasonal differences, the effects of alien disturbance remained evident. Dallas (1997) similarly found that, in the Palmiet and Berg Rivers, seasonal variation did not mask the effects of water quality impairment.

4.5. Abundance and richness of EPT+O taxa

Alien sites had the lowest abundance and morphospecies richness. This is in agreement with other studies that found low diversities and richness in alien vegetation in terrestrial ecosystems (Samways, *et al.*, 1996; Donnelly and Giliomee, 1985). Clearly, alien trees have a considerable effect on biodiversity.

Cleared sites indicated good recovery in terms of morphospecies richness and abundance, although both remained lower than in natural sites. Moreover, natural and cleared sites were never found to differ significantly, suggesting some measure of recovery of cleared sites in terms of overall abundance and richness. In addition, multivariate analysis of family-level abundances gave no significant difference between natural and cleared groups, suggesting recovery of invertebrate communities after clearing. At the morphospecies level, a significant difference was given for Rondegat River cleared and natural sites, but not Molenaars River sites, suggesting greater recovery of cleared sites in the Molenaars River. In fact, cleared sites along this river showed good regrowth of indigenous *Prionium*, trees and shrubs, while Rondegat River sites remained more exposed, with grass and sedges being more prominent.

Between-river and seasonal effects largely obscured the effects of alien invasion and clearing on macroinvertebrate assemblage patterns. Different taxa dominated in each river and during each month, their responses to alien disturbance thus also differing. Each river and month therefore had to be analysed separately to seek consistent patterns. The Ephemeroptera and Odonata appeared to be most sensitive to alien disturbance, while the Plecoptera and Trichoptera showed variable responses.

4.6. Community responses to alien invasion

Certain Ephemeroptera, Plecoptera, Trichoptera and Odonata are clearly harmed by aliens, having low abundances and incidences in alien sites. These included sensitive and endemic taxa, such as

the endemic teloganodid, *L. penicillata*, and the heptageniid, *A. harrisoni*, as well as a number of baetids, such as *P. bellum*, *B. harrisoni*, *D. capensis* and baetid C. Teloganodids and heptageniids are both grazers or scrapers that mostly feed on periphyton (Barber-James and Lugo-Oritz, 2003) and it is likely that the high degree of shading in alien sites prevents the growth of their food source, thus affecting populations.

Less sensitive taxa, such as coenagrionids and hydroptilids, were also harmed by alien invasion, being completely absent from alien sites. Coenagrionids use marginal vegetation as nursery and oviposition sites, thus being affected by the absence of this habitat in alien sites. Several taxa, such as the caenid, *C. capensis*, the hydropsychid, *Cheumatopsyche* sp. and the aeshnid, *Aeshna* sp., did not appear to be harmed or favoured by alien invasion, suggesting they responded to factors common to alien and natural sites, such as oxygen levels and the presence of riparian trees.

In contrast, many Trichoptera appeared to favour alien conditions, including the endemic and sensitive glossosomatids and barbarochthonids. In particular, the leptocerids within the *A. bergensis* group, together with *Ecnomus* and *Macrostemum*, were abundant in alien sites. The only ephemeropterans that appeared to benefit from alien conditions were the leptophlebiids, *Adenophlebia* and *Chloroterpes* B, while *Zygonyx* sp. was the only odonate to benefit. Notonemourids also had a higher abundance and incidence in alien sites.

The benefits these taxa gained from alien sites may have been related to food or habitat availability, or to water quality modifications (such as shading, lower temperatures and higher oxygen levels). Cummins *et al.* (1989) predicted that increased leaf litter availability would be followed by increased biomass of shredders. The greater availability of plant debris in alien sites may therefore have benefited shredders, such as notonemourids, leptocerids and barbarochthonids. In fact, shredders are known to be commonly associated with afforested and closed-canopied streams (e.g. Maridet *et al.*, 1998; Weatherley *et al.*, 1989).

Maridet *et al.* (1996) suggest that shaded, fast-flow conditions may be associated with an abundance of diatoms. They found a high abundance of both scrapers and diatoms in highly-shaded, high-velocity streams. Diatoms are an attractive food source to scrapers and are generally associated with low light intensity environments (Campbell and Doeg, 1989). Leptophlebiids are scrapers or collector-gatherers (Barber-James and Lugo-Oritz, 2003) that may have benefited from high velocity flows with cobbled substrates in the Molenaars River alien sites.

Most case-building trichopterans were not unduly harmed by alien invasion. It is likely that alien plant debris provided favourable material for case-building taxa, such as the *A. bergensis* group and *Cheumatopsyche* sp. It is also possible that certain taxa were responding to physical factors that were unrelated to alien disturbance, such as the cobbled substrate and the faster flow rates in the Molenaars River alien sites. Cobbled substrates are favoured by scrapers, such as caenids, leptophlebiids and glossosomatids (Davies, 1994), while *Zygonyx* is known to be strongly associated with riffles and rapids (Corbet, 1999).

4.7. Community responses to alien clearing

Certain taxa responded positively to alien removal, showing increases in abundance and incidence. In particular, the Odonata appeared to benefit, with only *Aeshna* sp. and *Pseudagrion* B not increasing in abundance after alien removal. Most odonates were, in fact, most abundant in cleared sites, with the exception of *Aeshna* sp., *Pseudagrion* A and *Anax* sp., which were all more abundant in natural sites. Only Coenagrionidae and Aeshnidae had the highest incidence in natural sites.

In addition to the Odonata, hydroptilids, leptocerids (*A. bergensis* C and *L. helicotheca*), baetids, teloganodids (*L. penicillata*) and leptophlebiids (*E. elegans*) appeared to benefit from alien removal. Heptageniids (*A. harrisoni*) also benefited, although this was only evident in March.

Alien removal exposes the river to increased sunlight, thus facilitating the growth of macrophytes, algae and periphyton. This may have considerable consequences for food webs and faunal composition. Where riparian vegetation has been removed, autotrophy plays a more important role (Bunn, *et al.*, 1997), while macrophytes contribute very little to food webs (Bunn and Boon, 1993). Macrophytes are, however, utilised by leptocerids (for food and shelter), hydroptilids (for shelter) and Odonata (for shelter and oviposition sites) (Maridet *et al.*, 1998). It is not surprising, therefore, that these families occurred mainly in cleared sites that had an abundance of marginal vegetation, including *Prionium*, grass and sedge. Adult Odonata have also been found to respond to the presence of these plant biotopes (see chapter 2 of this thesis).

Taxa may also have benefited from water quality or habitat conditions, modified as a result of alien clearing. Gomphids, for example, burrow into sandy substrates (Corbet, 1999) and were probably associated with the prevalence of sandy habitats in cleared site. Similarly, gravel substrates may have favoured collectors, which are often associated with these substrates (Davies, 1994). Certain leptocerids may have responded to the greater availability of grass for case construction, while the collector-gatherers such as leptocerids, baetids and leptophlebiids, may have benefited from the higher levels of suspended solids found in cleared sites.

Many taxa appear to have been harmed by clearing, their post-clearing abundances being lower than in natural sites. These included taxa that were mostly associated with trees, whether alien or indigenous, such as notonemourids, ecnomids, the caenid, *C. capensis,* the hydropsychid, *Cheumatopsyche* sp., the aeshnid, *Aeshna* sp., the sericostomatid, *Petroplax*, and the leptocerid, *Athripsodes* C. Several other taxa, mainly trichopterans, were also negatively affected. Zavaleta *et al.* (2001) point out that, while invasive plant species may provide usable food or habitat for indigenous fauna in the absence of original vegetation, the rapid removal of these invader species, without restoration of indigenous vegetation, might leave this fauna without food or habitat. The

sudden reduction in litterfall is therefore likely to affect energy flow, faunal composition and the overall functioning of the river (Muotka and Laasonen, 2002).

It is also likely that taxa were affected by sudden changes in water quality variables (such as increased temperatures and suspended solids or decreased oxygen levels), together with greater fluctuations in these variables and greater exposure to extreme values. Vuori and Joensuu (1996), for example, found that logging of forests in Finland resulted in increased sand, silt, turbidity and suspended solids, which greatly affected plecopteran populations. They also found a decline in shredders and an increase in filter feeders. This may explain the low abundance of notonemourids and barbarochthonids in cleared sites (only two notonemourid individuals, versus twelve in alien sites). Vuori and Joensuu (1996) also found that high silt loads in streams adjacent to logging areas disrupted the nets of filter-feeding hydropsychids, this possibly explaining the low abundance of hydropsychids in cleared sites in this study.

4.8. Response of endemic taxa

Recovery of endemic populations appears to be limited as abundances and incidences in cleared sites never matched those in natural sites. Endemic taxa were harmed by either alien invasion or alien clearing, or by both. Conversely, certain endemic taxa benefited from clearing, while others appeared to benefit from, or at least not be harmed by, alien invasion.

The sensitive sericostomatid, *Petroplax*, and the leptocerid, *Athripsodes* C, were harmed by alien invasion and again, to an even greater extent, by alien clearing. The sensitive teloganodid, *L. penicillata*, and the leptocerid, *L. helicotheca*, were harmed by alien invasion but showed some recovery after clearing. The leptocerid, *A. bergensis* C, also benefited from clearing. It appears that glossosomatids and barbarochthonids benefited from alien invasion, while the effects of clearing appear to be detrimental, although the small number of individuals encountered renders this uncertain.

As mentioned earlier, tolerant, widespread taxa appear to be the first to recover after alien clearing. King and Schael (2001) noted that disturbed rivers lost their signiature identities, perhaps through the loss of sensitive species. The highly variable distribution of alien and cleared sites in the MDS of morphospecies abundance (Fig. 11) supports this theory so that these sites probably reflect the more cosmopolitan and tolerant species.

The relative proportions of each vegetation type varied considerably across cleared sites, depending on the extent of recovery, the method of removal and the initial alien densities. This would have resulted in a more patchy distribution of invertebrate assemblages across sites and, therefore greater variability. However, cleared sites with short indigenous bushes and *Prionium* as dominant vegetation type were grouped with natural sites in the MDS, while sites with grass as dominant vegetation type were highly variable and were grouped with alien sites. This suggests that recovery of the sensitive, endemic taxa is delayed after clearing and, in fact, only occurs after the recovery of indigenous *Prionium* and fynbos.

4.9. Environmental variables affecting faunal distribution patterns

Factors affecting benthic macroinvertebrates are numerous and interrelated (Wright *et al.*, 1984). There is a high degree of interaction, both directly and indirectly, between the major variables, and with non-water-quality variables (e.g. substratum, current velocity, insolation) (Dallas and Day, 1993), so that isolating the effect of a single variable is problematic. Between-river and seasonal factors dominated invertebrate responses in this study and, in addition, different environmental variables were important in each river.

The Molenaars River was, on average, deeper and cooler with stronger currents and higher oxygen levels than the Rondegat River. Therefore, physical factors mostly explained between-river and seasonal differences (depth, temperature, conductivity), while vegetational factors (indigenous bushes, *Prionium*, alien trees, sedge and grass and bank exposure), together with

width and oxygen, mainly explained distribution patterns within rivers and months. Oxygen concentrations probably interacted with vegetation type, with cool, shaded alien sites having higher oxygen levels than warm, sunlit cleared sites.

All the vegetational factors were related to alien disturbance, indicating that alien disturbance does indeed have an important influence on assemblage patterns within rivers and months. In fact, faunal distribution patterns appear to reflect a vegetational 'succession' of recovery after alien tree removal. Grass and sedge are the first to colonise newly-cleared sites, followed by *Prionium* and, finally, indigenous bushes and trees. Recovery of these vegetation types in cleared sites is followed by the recovery of the invertebrate communities associated with them.

The Odonata appear to follow this succession most closely, although adult Odonata may have a more pronounced response to plant biotopes (Samways, 1993a, b; see also chapter 2 of this thesis). Osborn and Samways (1996) similarly found that variables that represented different ecological successional stages influenced adult Odonata assemblage patterns at newly colonised ponds.

The fact that marginal vegetation types were more important than water chemistry or physical factors (with the exception of oxygen and width), indicates that invertebrate distributions were primarily affected by marginal habitats or plant-invertebrate relationships, and only indirectly affected by water chemistry. This agrees with the findings of Ormerod *et al.* (1987), while, in Welsh streams, sites were classified according to both marginal habitats and water chemistry (Rutt *et al.*, 1989; Wright *et al.*, 1984; Moss *et al.*, 1987). Rutt *et al.* (1989) noted that afforested areas with steep-sloping banks had 'harder' margins that were unfavourable as habitats for certain taxa, while sites with an abundance of herbaceous marginal vegetation supported specialist marginal taxa, such as Odonata. Alien disturbance clearly evokes a similar faunal response.

Habitat-specific effects on stream invertebrates have, however, not been widely investigated and may, in fact, be highly relevant. Roque *et al.* (2003), for example, found that mesoscales (such as pools, riffles and runs) were important for macroinvertebrates, particularly flow-sensitive taxa. In terms of alien disturbance, changes to the quality and quantity of marginal or substrate habitats may evoke a more consistent, reliable and measurable response by benthic macroinvertebrates than by water quality changes, as measured by SASS.

4.10. Seasonal effects on invertebrate abundance and distribution

Abundances were generally found to be higher in autumn (March), although this disagrees with King's (1983) findings that abundances were higher in summer (January) along the Eerste River. However, King (1983) collected fauna to a depth of ten centimetres and it is possible that vertical migration of invertebrates in the substrate is greater during hot summer months, therefore being missed in this study. Weatherley *et al.* (1989), for example, attributed higher autumnal abundances in Welsh streams to vertical migrations through the substrate to the surface, or the fact that sizes large enough for capture were attained.

Water temperature influences the rate of biological activity. Even moderate changes in temperature can affect growth rates and emergence times (Stubbs and Warren, 1991). Temperature probably interacts with day length to control emergence times and the length of emergence periods (King, 1982). Changes in temperature, such as is caused by alien disturbance, can therefore cue life-history changes at inappropriate times (Rutherfurd *et al.*, 2000a). For example, warmer water in cleared areas may encourage faster growth and earlier emergences. In alien areas, the low temperatures and shade may reduce metabolic rates, thus delaying emergences and increasing the time taken to reach maturity. King (1981), for example, found that 'winter communities' persisted for longer in upper river zones where temperatures were lower. It

is likely, therefore, that alien disturbance has far-reaching effects on seasonal patterns of emergence, growth and survival, ultimately affecting faunal composition.

4.11. Recommendations for clearing

Alien clearing programmes should incorporate two approaches: mitigation of impacts on water quality and active management according to biodiversity and conservation objectives. Mitigation of water quality impacts should focus on: (1) preventing erosion of cleared banks, thus reducing levels of suspended solids, salinity and sand, and (2) cultivating indigenous fauna to stabilise banks, moderate temperatures and provide shade. This will result in elevated oxygen levels, this having an important effect on faunal assemblages. The re-establishment of indigenous riparian vegetation would also restore food web imbalances by restoring allochthonous input of organic debris (Bunn *et al.*, 1997).

4.11.1. Recommendations for maintaining water quality

Soil may be damaged by post-clearing fires and high intensity fires, in particular, can result in greater erosion. It is therefore important to use low intensity fires (e.g. burning during the wetter winter months). Steps should also be taken to stabilise banks after fires by sowing to accelerate post-fire vegetation recovery (Holmes and Marais, 2000).

In extreme cases, banks should be stabilised against erosion with physical structure, such as rocks, wood or stone, or with vegetation. Bank stabilisation is particularly crucial in cases where steep banks may inhibit the growth of marginal vegetation, thus increasing bankside erosion and reducing the availability of marginal habitats (Rutt *et al.*, 1989).

In high velocity situations, or where riverbanks are steep, it may be necessary to combine revegetation with bio-engineering approaches (Uys, 2003). Temporary sand traps may be useful for trapping eroded sediment, while bank stabilisation can be achieved with bioengineering

structures. These structures may include soft biotechnical techniques using geotextiles, which provide a more natural appearance than hard engineering techniques, such as rockpiles or groynes and rock revetments (see King *et al.*, 2003 for a description of these methods).

However, the technology used should be approriate for the specific scenario (e.g. bioengineering may only be practical in urban areas). The bank stabilisation methods used should also always be based on an understanding of natural hydrological and ecological processes. That is, where active erosion takes place naturally, bank stabilisation may cause more harm than good (Kondolf, 1998).

Revegetation of riparian zones will stabilise eroding banks, as well as provide shading to the river, thus maintaining water temperatures and dissolved oxygen levels. Revegetation will also provide habitats for both adults and larvae. *Prionium* is an efficient bank stabiliser and is preferred as an indigenous species, although hydroseeding of steep banks with non-invasive grass or herbaceous species may also be beneficial (Holmes *et al.*, 2000; Levitt, 1997). While *Prionium* contributes greatly to bank stabilisation and erosion prevention, cultivation of fynbos shrubs and trees will contribute to the cohesion and stability of steep banks, especially if they have rigorous rooting characteristics (McCann and Lindley, 1998). Native species are always preferable as they support local fauna by providing food, habitat or shelter. According to Henderson (1986) these species should withstand inundation, provide protection to banks throughout the year and be able to become established in adverse soil conditions, such as soil modified by long-term alien stands.

Rehabilitation of cleared riparian zones using cultivation of indigenous plants needs to be carefully planned and based on a sound understanding of environmental conditions of the sites and the ecological requirements of the cultivated species (King *et al.*, 2003). Holmes and Richardson (1999) recommend that indigenous seed should be sown in early autumn to augment recruitment from persistent seed banks, while Levitt (1997) described the methods used to

cultivate *Prionium* and other fynbos species from cuttings, after road construction in Du Toitskloof.

Unassisted recovery of vegetation may be possible if seed banks of indigenous species are preserved and germination encouraged. According to King *et al.* (2003), recovery of cleared areas along the Lourens River, Western Cape, would occur unaided as long as further disturbance was avoided. This would require maintaining a clear boundary zone along the river with no stacking or burning. Post-clearing fires, depending on the intensity, may damage indigenous seed banks, while injudicious application of herbicides may damage indigenous seedlings (Holmes *et al.*, 1987). Holmes *et al.* (2000) also found that the 'fell and burn' method of clearing had the greatest negative effect on the survival of plant guilds. This method of clearing results in high intensity fires that destroy seed banks, resulting in altered plant communities. Where possible, the 'burn standing' or 'fell, remove and burn' methods should be used, together with post-fire sowing. Wright (1993) also points out that fires may eliminate indigenous host plants for many years, thus reducing seed banks, so it may be important to ensure that, where indigenous vegetation occurs in cleared areas, it is not burnt during fires.

Dense stands of alien trees may also modify the soil to make it unsuitable for the recovery of indigenous plant species. For example, soil nutrient content may increase through higher annual litterfalls, these conditions not being favourable for fynbos re-establishment. Pienaar *et al.* (2004, unpublished report) found that indigenous vegetation is not able to establish itself on deeper, sandy soils associated with *Acacia* trees, indicating that intervention is necessary. Holmes and Marais (2000) also found that sites with a longer history of alien invasion may require sowing to accelerate recovery.

Stubbs (1991) found that modification of banksides along one side of the river only often mitigates the negative effects of vegetation removal. In Australian streams, the provision of 50%

shading is reportedly sufficient for significantly improved ecological function (Bunn *et al.*, 1999). Although this may not be transferable to South African rivers, it may nevertheless be worth considering clearing only one side of a river until the indigenous vegetation is at least partially established. This would prevent extreme changes in factors such as shade, temperature and dissolved oxygen.

It would also be advisable to remove alien trees before they become too dense, so that that the sudden changes in conditions is less extreme. There is a greater chance of indigenous fynbos species surviving in these less-dense alien stands and these can then be preserved to provide shade after the alien trees have been removed. In all events, regular follow-ups would be crucial.

4.11.2. Conservation and biodiversity considerations

Zavaleta *et al.* (2001) comment that, although there is a need to continue to develop eradication methodologies, there is also a need to integrate this into a more holistic restoration goal in the whole-ecosystem context. Vane-wright (1993) predicts that the 21st century will be considered the age of restoration biology as we try to achieve biodiversity and sustainability objectives. Restoration ecology is a growing field of research and management and is expected to increase in importance (Soulé, 1989). Rivers, being self-regulatory systems, are able to withstand a considerable amount of disturbance and then recover with a minimal amount of assistance once the disturbance is removed (Allan and Flecker, 1993). For this reason, river restoration can be viewed as a process of recovery enhancement (Gore, 1985). This generally focusses on rehabilitation of both the physical habitat and water quality. Restoration also needs to be integrated into catchment management, with monitoring as an essential component.

It should be remembered, however, that restoration is far more expensive than maintaining an ecosystem intact in the first place (Stork and Samways, 1995). The Australian principles for stream rehabilitation (Rutherfurd *et al.*, 2000a) consider protection to take precedence over

restoration. That is, protect undisturbed and biodiverse reaches from disturbance first, then rehabilitate, starting with reaches that will recover soonest with the least interference.

Alien clearing programmes in the Western Cape currently focus on the physical aspects of restoration at the expense of the bigger biodiversity picture. To achieve biodiversity objectives, emphasis needs to be given to restoration of water quality and habitats, protection of biodiverse areas, prioritisation of areas for clearing, integration into catchment management and long term monitoring of cleared sites.

4.11.2.1. Post-clearing restoration[1]

River rehabilitation is in its infancy in this country and major limitations include lack of research attention, inadequate attention to scientific method, failure to adopt bio-engineering approaches and lack of planning and structured rehabilitation processes (Uys, 2003). This is largely due to the lack of available information upon which to base decisions and a lack of post-clearing monitoring. More emphasis need to be placed on prioritising areas for clearing or rehabilitation, setting restoration objectives, planning the rehabilitation process and monitoring recovery (Kondolf and Micheli, 1995; Rutherfurd *et al.*, 2000a; Uys, 2003). Rehabilitation needs to incorporate a full planning, implementation and evaluation procedure (King *et al.*, 2003; Uys, 2003).

Eradication of aliens alone might be insufficient for full ecosystem recovery (Zavaleta *et al.*, 2001). The focus is often on 'structural restoration endpoints', such as species richness and diversity (Muotka and Laasonen, 2002), rather than the restoration of ecosystem processes ('functional endpoints'). Rather, restoration objectives should be based on both structural and functional components in the river channel and the riparian zone. If the functional integrity can be restored then an increase in biodiversity will follow (Downes *et al.*, 2002). Restoration of rivers

[1] The terms 'restoration' and 'rehabilitation' are used interchangeably to mean improving the ecological integrity of a disturbed river. For strict definitions see King *et al.* (2003).

therefore focusses on the reintroduction of appropriate habitat, assuming this will be followed by the desired biological response and improved ecological functioning (Rutherfurd *et al.*, 2000a; Usher and Jefferson, 1991). This requires knowledge of the habitat requirements of the target fauna (Downes *et al.*, 2002).

Because habitat loss is a major cause of biodiversity loss (McNeely *et al.*, 1995), the maintenance of habitat quality is of vital importance for biodiversity conservation (Allan and Flecker, 1993). Measures aimed at restoring or maintaining habitat conditions would benefit both biodiversity and ecosystem function. Physical habitat for aquatic macroinvertebrates spans a range of spatial scales, including the influence of riparian vegetation on community structure and function, the abundance of wood available for wood-dwelling species, the nature of the stream-bed and the interactions between substrate type, current strength and water depth (Campbell, 1994). All these factors vary temporally, making it difficult to classify habitats. As a result, very little is known about the specific habitat requirements of benthic invertebrate species (Campbell, 1994), which makes it difficult to set restoration objectives. Restoration of instream habitat therefore usually involves reinstating the natural flow, substrate or vegetation conditions.

This study showed that the recovery of benthic macroinvertebrate communities followed the recovery succession of riparian vegetation. More specifically, the recovery of sensitive, endemic taxa followed the recovery of indigenous plant species. Therefore, the rehabilitation of indigenous riparian vegetation is likely to be followed by the recovery of invertebrate biodiversity.

In fact, revegetation would restore both water quality and of plant biotopes. Riparian plants would provide habitat for marginal species and organic input for shredders and other herbivores, while also helping to stabilise the bank and prevent erosion, reduce sediment input and stabilise temperatures. Because different life cycle stages have different habitat requirements, restoration

of riparian plants needs to consider water quality and aquatic habitats for egg and larval stages, and riparian habitats for aerial adult stages (Fry and Lonsdale, 1991).

Habitat diversity promotes species diversity. Moreover, there is a positive relationship between plant diversity and species diversity (Stubbs and Warren, 1991). The restoration of biodiversity in cleared sites should therefore also focus on providing a diversity of plant biotopes by cultivating or maintaining different vegetation types (*Prionium*, shrubs, trees, sedge), species and ages. Brown and Southwood (1983), for instance, found that arthropod diversity and abundance increased with plant succession from grassland to shrubs in an abandoned arable field. Therefore, management of successional stages has often been suggested as a means of maintaining diversity for insect conservation (Samways, 1994). Donnelly and Giliomee (1985), for example, showed that ant biodiversity in fynbos was achieved by maintaining a mosaic of successional ages using fire as a management tool. In this study, riparian vegetational recovery also reflected a succession that increased in structural complexity with age. It may therefore be useful to facilitate this succession by active cultivation of each vegetation type, thus facilitating the attainment of biodiversity goals.

In addition to promoting overall diversity and abundance, care should be taken to maintain or restore habitats required by rare, stenotopic, sensitive and endemic taxa. For example, the endemic damselfly, *Pseudagrion furcigerum* (probably *Pseudagrion* A in this study) is often associated with *Prionium* (see chapter 2) and would benefit from active cultivation thereof. Similarly, the endemic teloganodid, *L. penicillata*, and the sericostomatid, *Petroplax*, were clearly associated with indigenous fynbos in natural sites. They would therefore benefit from the maintenance or cultivation of indigenous fynbos, including bushes and trees.

4.11.2.2. Protection and prioritisation

Stream rehabilitation programmes in Australia have adopted a general principle that protection of healthy streams should always take precedence over rehabilitation and that rehabilitation should be integrated into catchment management (Rutherfurd *et al.* 1998). 'Corridor reserves' have been identified (Bennett, 2003), these being corridors of riparian habitat that link important conservation areas, thus providing potential dispersal pathways that can maintain connectivity between populations. New (1993) recommended that centres of endemism and diversity be identified for such protection. It is essential, therefore, that alien clearing programmes identify highly biodiverse areas for protection against alien invasion.

In addition to prioritising areas for protection, rehabilitation efforts should incorporate a planning phase whereby areas are prioritised for clearing and restoration. For example, lightly-infested and newly-invaded areas should be prioritised as they can often recover fairly well without intervention (Holmes and Marais, 2000). This is because, firstly, they are likely to contain more species and recovery is less likely to need intervention where biodiversity is high (Uys, 2003). Secondly, there are a greater number of indigenous seeds in the soil and, therefore, more that are able to germinate after clearing (Holmes and Marais, 2000). Finally, there may be surviving fynbos species that can be preserved, circumventing the need for cultivation. Where these areas occur close to natural areas, recovery may be facilitated by recolonisation by indigenous fauna and flora (Bell *et al.*, 1997; Williams, 1997).

4.11.2.3. Integration into catchment management

Morley and Karr (2002) comment that, to achieve meaningful long-term biological recovery, conservation and restoration efforts should extend beyond in-stream habitats to examine the effects operating across the entire catchment. That is, efforts to conserve and maintain

biodiversity need to operate at both the habitat level (to restore in-stream structure and function) and the landscape level (to prevent local extinctions and maintain metapopulations) (Roque *et al.*, 2003).

The definition of biodiversity conservation given by the International Union for the Conservation of Nature (IUCN) includes the maintenance of essential ecological processes and the preservation of genetic diversity. This would include processes such as dispersal, colonisation and gene flow, which are important in species persistence as well as in species formation. It is important to consider these processes at the scale at which they occur. For lotic organisms, this is at the catchment level (Morley and Karr, 2002; Saunders *et al.*, 2002; Willson and Dorcas, 2003; Wishart *et al.*, 2003). River restoration therefore needs to be integrated into catchment management.

Saunders *et al.* (2002) suggest that freshwater protected areas should ideally be located within intact catchments with natural hydrological regimes and an absence of exotic species. However, where this is not possible, conservation efforts should focus on the land immediately bordering freshwater ecosystems and the headwaters. The catchment-level approach was also recommended by Willson and Dorcas (2003), who found that the preservation of small riparian buffer zones was insufficient to maintain stream conditions for an abundance of stream salamanders, as land use throughout the catchment had a greater effect on populations.

While the catchment level encompasses all the complex components of biodiversity, sub-units, such as biotopes and habitats, are useful as additional components of management activities (Samways, 1993a). Insect conservation, for example, has focussed both on maintaining the biotope requirements of species and on preserving biotopes within various landscapes (Samways, 1994). The size of these landscapes, habitats and biotopes needs to consider the requirements for survival and the maintenance of genetic variation (Samways, 1993a).

Principles of landscape ecology may apply to restoration and conservation projects (Bell, *et al.*, 1997). Many of these principles are based on island biogeography theory (Mac Arthur and Wilson, 1967) which relates the number of species present in an island with island size and distance from a source of colonists. Where alien infestation occurs over large areas, and distances between indigenous riparian patches is greater than the average dispersal ability of the fauna, extinctions may follow (Zwick, 1992). That is, indigenous riparian habitats may form ecological islands within a sea of unsuitable alien habitat. This may result in isolated and fragmented populations at risk of extinction, a threat that may intensify under conditions of global warming (Samways, 1993b). As habitats become more isolated and fragmented, the chances of recolonising a site decreases and species may be permanently lost. Forest fragments left after alien clearing are more vulnerable to extinctions and maintain fewer plant species (Brokaw, 1998). The rate of extinctions is largely determined by the size of the island, its shape, configuration, distance from, and connectivity to, other populations (Bell *et al.*, 1997). Dispersal ability becomes important factor in faunal diversity, as immigration and colonisation rates are affected (Mac Arthur and Wilson, 1967). Wholly aquatic invertebrates (e.g. amphipods) are particularly at risk as recolonisation can only occur by drift into lower reaches (Zwick, 1992). Invertebrates with aerial adults may be less affected because of their ability to fly to adjacent streams, stronger fliers being more successful colonisers than weaker fliers. Dispersing adults are therefore able to form metapopulations across streams in a region (Zwick, 1992).

Where possible, extinctions from individual catchments should be avoided as dispersal across catchments is usually more difficult because of larger distances. Recolonisation often only occurs from source populations along the same river (Zwick, 1992, Morely and Karr, 2002). Zwick (1992), for example, found that relic populations of Plecoptera are unlikely to recolonise rivers where they have become extinct. Lowland rivers are particularly prone to this isolation as they are further from each other than headwaters (Zwick, 1992).

Ecological restoration therefore needs to focus on improving the continuity of river systems, both longitudinally along a single river, and horizontally between rivers in the same and in different catchments (Downes *et al.*, 2002; Noss, 1991). For Working for Water, this means focusing on protecting areas from invasion, maintaining connectivity between undisturbed areas and preventing landscape fragmentation. More specifically, alien clearing efforts should prioritise invaded areas that pose a risk of isolating populations in habitat fragments, so that local extinctions do not eventually become regional extinctions. In addition, indigenous habitats need to be protected to prevent habitat fragmentation from alien invasion. These habitats can then provide source populations for recolonisation of cleared areas.

To facilitate the dispersal of animals between otherwise-isolated habitat patches, linkages may be used. Linkages between patches may be achieved by continuous habitat corridors or discreet stepping stones of favourable habitat through the inhospitable (i.e. alien) matrix (Bennett, 2003). While stepping stones of cleared areas may be useful for the dispersal of the more mobile species of aerial adults, this would not necessarily ensure the survival of aquatic larvae or of taxa without aerial life-cycle stages (e.g. molluscs). Maintaining or restoring continuous corridors of indigenous riparian vegetation would therefore be more effective for aquatic macroinvertebrates.

Considering the immensity of the task, it may be worth considering partial clearing of one side of the river only to establish this connectivity and thus facilitate dispersal through alien areas. However, this riparian strip would need to be wide enough to provide favourable riparian and in-stream habitat in addition to being a path for dispersal, so as to benefit both aerial and aquatic taxa, irrespective of dispersal abilities. Water quality would also need to be maintained. Further research is required to test the effectiveness of this strategy as it would only be effective if it is properly maintained and if it provides for the habitat requirements of the fauna (Bennett, 2003). Furthermore, Rosenberg *et al.* (1997) warn that, while corridors may facilitate dispersal, the

extent to which they maintain biodiversity and prevent local extinctions remains uncertain. Landscape level approaches therefore remain the best approach.

4.11.2.4. Monitoring

No restoration attempts are complete without evaluation and monitoring. The *Global Biodiversity Strategy* (WRI/IUCN/UNEP, 1992) recommends that an early warning system be established to 'monitor potential threats to biodiversity and mobilise action against them'. Monitoring consists of intermittent (regular or irregular) surveillance to ascertain the extent of compliance with a predetermined standard or degree of deviation from an expected norm (Hellawell, 1991). Monitoring can therefore detect disturbance impacts on biodiversity so that action can be taken to prevent further loss or extinctions. That is, it provides information that can guide immediate and long-term management and conservation decisions. It can also be used to assess the effectiveness of past management actions.

Long-tem monitoring has become an essential requirement of biodiversity conservation and is usually used for detecting disturbance. Restoration is rarely monitored (King *et al.*, 2003). However, as ecosystem restoration increases in importance, monitoring of improving conditions is expected to become a central feature of biodiversity conservation (Stork and Samways, 1995). Lack of monitoring leads to repetition of mistakes and slow progress (Kondolf, 1998). Therefore tools need to be developed specifically to evaluate the rehabilitation process.

While alien clearing methods have been well documented, very little information exists on post-clearing recovery. Eradication alone may not necessarily be followed by ecosystem recovery. The process of alien clearing should therefore be integrated into a whole-ecosystem context, focussing on both restoration and assessment (Zavaleta *et al.*, 2001). Ideally there should be both: 1) pre-eradication assessment to strategise removal methods that will not have harmful ecological effects 2) post-removal assessment to inform restoration efforts.

A major problem with using benthic macroinvertebrates in monitoring is that each river and catchment has its own 'signiature' in terms of species composition (King and Schael, 2001), as was evident from the inconsistent responses across river systems and months. This makes it difficult to devise standardised assessment protocols and endpoints. Where taxa did show consistent responses across rivers and months, there was considerable overlap between disturbance regimes (Baetid C, *Cheumatopsyche* sp., *A. harrisoni* and *B. harrisoni*), making it difficult to use them in characteristic assemblages as it would require careful interpretation of relative abundance data. Therefore, each river and catchment would need its own assessment tools and endpoints. This notwithstanding, a number of detector taxa have been identified in this study that have the potential of being generally applicable, pending further research.

There is currently much debate about the definition of the term 'indicator' and what exactly an indicator should indicate (Simberloff, 1998). In general, an indicator should reflect some aspect of the environment in which it is found (McGeoch, 2002). Indicator species include characteristic species (Dufrêne and Legendre, 1997) that are not only specific to a habitat state but have a high probability of being sampled in that habitat (i.e. high fidelity and specificity). Therefore, in restored rivers, the appearance of an indicator species characteristic of natural, undisturbed sites (i.e. indigenous riparian vegetation) would indicate successful restoration.

Species may also be classified as detector species (Jenkins, 1971) if they have medium fidelity and medium specificity, so detect not only changes, but also the direction of those changes (McGeoch *et al.*, 2002). Thus, a decline in abundance of detector species may indicate increased disturbance (i.e. alien invasion), while an increased abundance would indicate recovery. Detector species are useful for longer-term monitoring within and across ecological states and determine directional changes, while indicator species can only be sampled in undisturbed or healthy conditions.

Potential detector species identified in this study included the teloganodid, *L. penicillata*, during March and April (i.e. autumn) and *A. harrisoni* and *P. bellum* during summer and autumn (January to April). *L. penicillata* is probably also present throughout winter, being observed by King (1982) to be a 'winter' species that was absent during hot summer months. These morphospecies can be expected to have a relatively high abundance and incidence in natural sites. In cleared sites, an increase in abundance and incidence would indicate recovering conditions, while, in natural or cleared sites, a decrease in abundance and incidence would indicate increased invasion.

According to the qualities of a good indicator species (Brown, 1991), all three species are appropriate as they have a high association with natural conditions, were relatively abundant, had a high ecological fidelity and appeared to respond rapidly and predictably to disturbance. In addition, *L. penicillata* is sensitive to changes in water quality (teloganodids scoring 12 SASS points) and is of conservation importance as an endemic species, thus being useful for identifying biodiverse areas requiring protection. It is also relatively easily identified as it is the only species within the genus and the genus is easily identified by eye in the field, having a row of long setae along the anterior margin of the head.

A. harrisoni was the only morphospecies identified within the Heptageniidae and the genus, *Afronurus*, is the only representative of the Heptageniidae in the Western Cape, therefore also being easily identified at least to genus level in the field. Like *L penicillata*, *A. harrisoni*, is sensitive to water quality changes (Heptageniidae scoring 13 SASS points) and is likely to be endemic to the region, as rare recordings of the species elsewhere are probably as a result of misidentification (King, 1982).

However, *P. bellum* is neither endemic, nor easily identified and its sensitivity to changes in water quality is not known. Identification would require the collection of all Ephemeroptera followed by

sorting under a microscope to at least genus level. The identification of baetids, in general, are problematic and identification to species level would probably require specialist input. This would clearly not be practical for rapid biomonitoring purposes and this species would only be useful for more in-depth ecological studies.

Far more practical and efficient would be to use family-level identifications during assessments. Families are easily identified and counted in the field, even by trained non-biologists. As *L. penicillata* and *A. harrisoni* were the only morphospecies identified within the Teloganodidae and Heptageniidae respectively, it follows that family-level identifications would be sufficient to detect alien disturbance or post-clearing recovery. Moreover, because *A. harrisoni* and *L. penicillata* occurred in relatively high abundances, it is unlikely that the findings would be unduly altered if additional species are found within these families. More detailed ecological studies may, however, require collection and identification of individuals to species level.

In addition to teloganodids being of conservation importance as endemics, both families are sensitive to water quality changes, therefore being highly suitable for monitoring. Of concern, however, are the seasonal fluctuations in their abundances. King (1982) considered A. *harrisoni* to be a 'summer species' so the use of the Heptageniidae may be less reliable in autumn. It may therefore be that, while heptageniids are most reliable as detectors during summer, teloganodids can only be used for monitoring during autumn (and probably winter).

Both teloganodids and heptageniids are grazers on periphyton, suggesting that their distribution may be linked to that of periphyton. This agrees with the findings of Muotka and Laasonen (2002) that abundance of periphyton-feeding scrapers increased in restored Finnish streams. Periphyton has, in fact been used by the United States Environmental Protection Agency for rapid bioassessment of streams and rivers (Barbour *et al.*, 1999) and it may therefore be worth investigating the possibility of using this method in the Western Cape.

Other potential detectors identified for natural sites at the family level included Aeshnidae during March and Baetidae during January. Gomphids were identified as potential detectors of change to cleared conditions during March. However, only Aeshnidae is considered sensitive to water quality changes (scoring 8 SASS points), while the sensitivity of baetids is determined by the number of species present in the SASS sample. Gomphids, being burrowing animals associated with sandy substrates, may be useful to indicate conditions of increasing erosion and sedimentation in cleared sites. However, the suitability of these taxa as detectors of alien disturbance or post-clearing recovery bears further investigation.

The Odonata may also be useful for monitoring the recovery of marginal vegetation as they are often associated with particular plant biotopes (Samways, 1993b). From this study, it was evident that a relatively high abundance of the coenagrionid, *Pseudagrion* A (probably the endemic *P. furcigerum*), would indicate natural or near-natural cleared sites with high levels of marginal *Prionium* and indigenous fynbos. Similarly, a relatively high abundance of *Pseudagrion* B (probably the more widespread *P. kersteni*) would indicate cleared sites with a dominance of *Prionium*. An abundance of the libellulid, *Trithemis* A (probably *T. furva*), can be expected in warm, sunlit, cleared sites with an abundance of marginal grass, sedge and reeds. An abundance of *Orthetrum j. capicola* would indicate newly-cleared sites that are still dominated by grass and sedge, while *Aeshna* sp.(probably *A. subpupillata*) can be expected to be relatively abundant in sites with an abundance of trees and bushes. If the probable species names have been correctly applied to the odonate morphospecies identified, this would support the observation that endemic taxa are associated with indigenous vegetation, as both *A. subpupillata* and *P. furcigerum* are endemic species associated with indigenous trees and *Prionium* respectively (see chapter 2).

Because larval Odonata respond to both submerged marginal vegetation structure and water quality conditions (Samways, 1993b), they could be useful for monitoring in-stream biotope quality in addition to water quality measures using SASS. Not only are they fairly biotope

specific, but they are also fairly easily sampled, being relatively large, and are usually present throughout the year (Corbet, 1999). They are also ubiquitous generalist feeders, therefore being independent of the presence or absence of other taxa (Samways, 1993b). However, identification to species level is often difficult, particularly for early instars, and this limits their usefulness in monitoring. Bigger sample sizes may also be required as only a few Odonata are sampled in SASS samples, resulting in greater variability and inconsistencies. Because of these difficulties, it would probably be more feasible to monitor adult Odonata assemblages (see chapter 2). However, adults are only active during summer so that sampling of larval assemblages may complement adult findings during the rest of the year. Further investigation using larger samples throughout the year may be worthwhile.

Another useful monitoring tool may include assessing the relative incidence of high-scoring and low-scoring SASS taxa. Cleared sites generally have a relatively higher incidence of widespread, eurytopic taxa, so that, as these sites recover to a natural condition, the incidence of sensitive high-scoring taxa can be expected to increase. This would include many stenotopic, endemic taxa, including teloganodids.

Whichever monitoring method or indicator taxon is selected, rigorous testing across rivers and months is required to establish its reliability. Indicator and detector taxa need to be tested in different rivers with different flow regimes over several years to ensure they are geographically and temporally robust (McGeoch, 1998). The results presented here apply only to the Western Cape during summer and autumn (January and March). It is unclear whether these results will hold true for all Western Cape rivers, or at other times of the year. It would also be necessary for specialist confirmation of identifications given to morphospecies.

From species accumulation curves, it is recommended that a minimum of twenty samples be taken from each disturbance regime to adequately represent the community. Data obtained in

March is also likely to be more informative and reliable, simply because abundance and richness were greater and all indicator taxa (including the endemic, *L. penicillata*) are available to provide a more detailed assessment. Finally, to prevent the effects of pseudoreplication (Hurlbert, 1984), it is recommended that, where possible, the Before-After-Control-Impact design suggested by Stewart-Oaten *et al.* (1992) be applied during monitoring.

There are many linkages that can be made between all aspects of river rehabilitation (i.e. planning and prioritisation, integration into catchment management, assessment and monitoring) and present organisational and governmental programmes, so that an interdisciplinary, ecosystem- and catchment-based approach can be adopted. The South African River Health Programme (RHP), for example, has been assigned the task of developing the procedures and infrastructures for implementing ongoing biomonitoring on a national scale (Dallas, 2000). The RHP regularly uses SASS, together with the Riparian Vegetation Index (Kemper, 2001), to assess river health. Prioritisation decisions can be linked to procedures to determine Resource Directed Measures (RDM), such as determining the Present Ecological Status and assigning Ecological Reserve Categories and Management Classes (from DWAF, 1999). These RDM methodologies are, in effect, prioritisation procedures that are equivalent to assigning a protection status to rivers and these can be extended to accommodate prioritisation for clearing or rehabilitation (Uys, 2003). Linkages can also be made between river rehabilitation and Catchment Management procedures, such as the Integrated Management Process.

4.12. Taxonomic resolution

Identifications to species level are often required for ecological analyses (Resh and McElravy, 1993) and are important for estimating population sizes to determine the rarity/threatened status of species. Species inventories are useful for identifying areas of endemism, for evaluating areas for protection and for meeting biodiversity management objectives (Stork and Samways, 1995).

In fact, international agreements, such as the Convention on Biological Diversity and *Agenda* 21, have called for the world's biodiversity to be inventoried and monitored (Stork and Samways, 1995).

However, species-level identifications, particularly of aquatic macroinvertebrates, are often fraught with taxonomic difficulties and inconsistencies, making this a time-consuming, expensive and often unreliable assessment tool, particularly for rapid bioassessments. For example, it was only recently discovered that the notonemourid, *Aphanicercella barnardi*, actually consisted of five morphologically and geographically discreet forms (Stevens and Picker, 1999).

In contrast, family-level identifications can be achieved relatively easily in the field. In this study, family-level counts took about three days, compared to about four weeks for species-level counts under a microscope, with a limited availability of taxonomic information. However, in terms of ecological information gained, the return for effort was minimal. Therefore, if found to provide meaningful ecological information, family-level identification is more feasible. It also allows for reliable comparisons with other studies even where different sampling methods have been used (Bournaud *et al.*, 1996). Family-level identification would also allow for a larger number of invertebrate taxa to be analysed relatively easily, including those that require specialist input (e.g. Diptera, Coleoptera). Moreover, so little is known of the distribution of species, let alone conclusive identifications, that species-level identifications can often lead to unreliable interpretations. Instead, it may be valuable to select a few species that can provide meaningful information on community processes (e.g. endemic, sensitive, typical or indicator species.)

This study found that morphospecies data (of EPT and Odonata taxa) had the greatest power to discriminate between disturbance regimes, while family-level presence/absence data (of all SASS taxa) had the least discriminatory power. This is because presence and absence data give equal weight to common and rare taxa. Presence/absence data only distinguished natural sites from alien

sites. However, when used in conjunction with SASS, presence/absence data provided a useful method of assessing, not only water quality, but also the relative proportions of sensitive and endemic versus tolerant and widespread taxa, thus giving a qualitative assessment of river health and biodiversity.

Abundance data clearly increased the power of discrimination and several SASS taxa may emerge as potential indicators of natural conditions if multivariate analysis of abundance data is performed. These taxa include Helodidae, Athericidae and Corydalidae, all of which had high incidences in natural sites. Various hemipterans (e.g. Gerridae, Notonectidae and Corixidae) had high incidences in cleared sites and, if found to also be abundant in cleared sites, may be useful as indicators of cleared conditions. This bears further investigation as all these taxa would be easily identified and counted in the field, making it feasible to use them for biomonitoring.

However, for more detailed community responses multivariate analysis of abundance data is more informative. In this study, morphospecies abundances were most effective at classifying sites according to disturbance. However, this method was extremely time-consuming and laborious. Family-level abundances, on the other hand, was relatively straightforward and was still able to detect disturbance effects, although natural and cleared sites were not as clearly distinguished. It also allowed for the identification of detector families (Teloganodidae and Heptageniidae) that can be used in rapid bioassessments. Both are easily identified and counted in the field.

Therefore, family-level identification appears, not only to provide sufficient ecological information, but also to be the most practically feasible. That is, the family-level data probably represented the best compromise between the cost and effort of collection and processing, and the information content of the resulting data. This is in agreement with other authors that have found family-level identifications to be sufficient (Bournaud *et al.*, 1996; Brown, 2001; Dallas, 1995, 1997; Furse *et al.*, 1984; King, 1982; Rutt *et al.*, 1989). Furse *et al.* (1984) similarly found

species-level identifications to be more reliable and accurate, but family-level identifications to give comparable results.

Although family-level responses were sufficient to detect disturbance, morphospecies responses to disturbance were far more evident. This did not, however, agree with other authors that have found community responses to disturbance to be more evident at family than species level because the natural environmental 'noise' is less evident (Brown, 2001; Warwick, 1993). Bournaud *et al.* (1996) found that species and families showed similar responses in disturbed sites only.

Neither presence/absence nor family-level identifications provide information on species richness and little information on conservation considerations such as endemicity or rarity. Measures of species richness and diversity often use quantitative indices. These have been reported to be seriously underestimated at the family level, compared to the genus or species level (Guerold, 2000). However Guerold (2000) cautions that, for richness and diversity indices, considerable information is lost leading to unreliable interpretations of indices.

As Stork and Samways (1995) point out, biodiversity management is not just about numbers of species, but also about processes, such as the proportion of stenotopic endemics versus eurytopic widespread species (Samways, 1994). Identification to species level may, therefore, be useful to identify rivers that should be protected from alien invasion or prioritised for clearing. *L. penicillata*, in particular, would be useful as it is easily identified and is a sensitive, endemic species that may be useful for identifying biodiverse areas, or for assessing recovery according biodiversity objectives.

Species-level identifications are also useful for more detailed community studies. In this study, the greater resolution provided by morphospecies-level identifications gave a number of additional findings not evident at family level. For example, the ephemeropteran, *P. bellum*, was

identified as a potential detector species. Also shown was the extent to which responses to alien disturbance vary within each family. This appears to be somewhat related to food and habitat requirements of the individual species, this information being lost at the family level. Morphospecies abundances also provided more accurate information on invertebrate responses to environmental variables.

Therefore, while SASS and family presence/absences provide rapid, qualitative initial assessments, abundance data is more useful for quantitative community responses. Multivariate analysis of family-level abundance data is sufficient for detecting alien disturbance, while the families, Teloganodidae and Heptageniidae, may be useful in rapid bioassessments. However, where more detailed information is required regarding community responses and conservation objectives (e.g. evaluating typicalness, biodiversity, rarity), morphospecies identifications may be more reliable. The species *L. penicillata* and *A. harrisoni* may also be used to confirm family-level findings. Guerold (2000) suggested using family-level identifications for detecting changes only and species-level identifications to analyse the extent or nature of the perturbation. Similarly, Furse *et al.* (1984) recommended the use of family-level data for monitoring programs and for classifying sites and species identifications for predictive studies and for determining conservation objectives.

4.13. Suggested further research

Further research would be essential to establish the seasonal and geographical reliability of indicators and detectors, in particular, teloganodids, heptageniids and *L. penicillata.* It would also be necessary to establish how other species within the Teloganodidae and Heptageniidae are affected by alien disturbance.

The absence of larvae of Platycnemidae and Synlestidae (Odonata) is curious as the adults were observed to be fairly abundant, at least along the Molenaars River. The absence of the larvae may

indicate inadequate sampling, seasonal emergence patterns or the effects of disturbance. Because these families include endemic and rare species, such as *Chlorolestes umbratus* and *Allocnemis leucosticta*, it would be important to investigate the reason for their absence. Moreover, more comprehensive sampling of the Odonata may elucidate assemblage patterns that may be useful for monitoring biotope recovery or degradation during winter months when adults are absent.

On a landscape level, the role of corridors is uncertain (Haddad, 2000). Therefore, the effect of riparian zones as linkages between habitat patches should be investigated. For example, would clearing one side of the river only promote dispersal and reduce habitat fragmentation?

The effect of alien disturbance on seasonal life histories has not been determined. This may have profound effects on invertebrate communities and survival of sensitive or endemic taxa. Disturbed sites appear to be more susceptible to seasonal effects, showing greater seasonal variability in water quality. Moreover, for monitoring and assessment purposes, it would be important to establish which month yields accurate information with the least variability.

The effect of exotic fish on community patterns was not assessed in the present study. Exotic trout and bass occurred in the Molenaars River and may have decreased the abundances of Plecoptera and Trichoptera, as has been documented in Australia (Fletcher, 1979). In English streams, brown trout has been found to reduce the densities of the predatory trichopteran, *Plectrocnemia conspersa* (Schofield *et al.*, 1988).

Weatherley *et al.* (1989) found rapid recovery after perturbation in Welsh streams and attributed this to faunal movements deeper into the substratum during disturbance events, allowing rapid recolonisation of denuded areas. Sampling of interstitial areas, particularly in the warmer, unshaded, cleared sites, may provide a more complete description of faunal response to alien disturbance. Maridet *et al.* (1996), for example, found that 70 % to 96 % of invertebrates were found within the first 15 cm of the substrate.

The effects of reduced litterfall in cleared areas have not been determined but may provide insight into faunal responses to alien clearing. Muotka and Laasonen (2002), for example, found low leaf retention in restored streams and they suggested the introduction of structures (e.g. tree trunks) that would increase leaf retention and therefore the organic food content of the water. They also devised a method of assessing restoration based on leaf retention, stream habitat and macroinvertebrate communities.

Finally, assessment based on processes may be a more direct method of assessment of the effects of alien disturbance on ecosystem function and river health. These ecosystem processes may include energy pathways, nutrient cycling and community metabolism (Bunn, *et al.*, 1999; Davies, 1994). For example, increased exposure to sunlight as a result of alien clearing may result in higher levels of autotrophy (Gasith and Resh, 1999). Williams (1997) found an abundance of detritivores at restored riparian sites, while the abundance of predators was relatively low and that of herbivores declined. Methods used to analyse energy pathways and community metabolism are reportedly relatively rapid and inexpensive and provide accurate information on the restoration or decline of river ecosystems following riparian modifications (Bunn, *et al.*, 1999).

In this study, invertebrate responses often appeared to reflect patterns of food availability, particularly with respect to plant debris and algae (including filamentous algae, periphyton and diatoms). It may therefore be useful to assess the effect of alien disturbance on the distribution of food types relative to the distribution of associated invertebrate functional feeding groups. Periphyton may also prove useful in bioassessments.

5. Conclusion

Removal of alien vegetation by the Working for Water programme appears to have evoked a positive response by benthic invertebrate communities, as both abundance and species diversity increased after clearing and faunal assemblages, at least at the family level, resembled those in

natural sites. However, in terms of water quality, several sensitive and endemic families appear to decline after alien clearing, being replaced by more widespread, eurytopic families. Alien clearing appears to bring about sudden and dramatic increases in water temperature, suspended solid concentrations, conductivity and sand, and a decline in oxygen and litterfall.

To conserve biodiversity, as opposed to merely restoring abundance, endemic and stenotopic taxa need to be protected and maintained. Because both water quality and habitat quality are of vital importance to the preservation of biodiversity, it is recommended that Working for Water address water quality issues and incorporate river restoration into alien clearing and catchment management practices. That is, there needs to be a shift in emphasis from strict alien control to ecosystem restoration. In particular, the maintenance and cultivation of indigenous vegetation is important to encourage the recovery of endemic, sensitive taxa, thus increasing overall biodiversity. Ideally, river restoration needs to set catchment-level objectives but act at a local scale for manageability (Uys, 2003) and protection should always take precedence over clearing.

Finally, no restoration process is complete without ongoing monitoring and assessment. For this, Teloganodidae and Heptageniidae may be useful in rapid bioassessments, pending further research. The endemic teloganodid, *L. penicillata*, may also be useful for prioritising areas for protection or clearing, based on biodiversity objectives. In addition, SASS may be useful for assessing overall river health, but interpretation of scores according to alien disturbance must be done with caution. Ideally, SASS should be used only as an initial assessment of disturbance, followed by more specific indicators, such as Heptageniidae and Teloganodidae, that can interpret these changes in terms of alien invasion or post-clearing recovery. Used in conjunction with other biotic groups, such as vegetation or adult Odonata, a more complete assessment of ecosystem integrity will be achieved.

References

Allan, J.D., Flecker, A.S. 1993. Biodiversity conservation in running waters. BioScience 43(1), 32-43.

Armitage, P.D., Moss, S.D., Wright, J.F., Furse, M.T., 1983. The performance of a new biological water quality score system based on macroinvertebrates over a wide range of unpolluted running-water sites. Water Research 17, 333-347.

Barber-James, H.M., Lugo-Oritz, C.R., 2003. Chapter 2: Ephemeroptera. In Freshwater Invertebrates of Southern Africa Volume 7: Insecta I; Ephemeroptera, Odonata and Plecoptera. ed I.J. de Moor, J.A. Day, F.C. de Moor, pp. 16-142. WRC Report No. TT 207/03. Water Research Commission, Pretoria.

Barbour, M.T., Gerritsen, B.D., Snyder, B.D., Stribling, J.B., 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish. Second edition EPA 841-B-99-002. U.S. Environmental Protection Agency; Office of Water; Washington, D.C.

Bell, S.S., Fonseca, M.S., Motten, L.B. 1997. Linking restoration and landscape ecology. Restoration Ecology 5(4), 318-323.

Bennett, A., 2003. Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation. IUCN, Gland, Switzerland and Cambridge, UK.

Bournaud, M., Cellot, B, Richoux, P., Berrahou, A., 1996. Macroinvertebrate community structure and environmental characteristics along a river: congruity of patterns for identification to species or family. Journal of the American Benthological Society 15(2), 232-253.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecological Monographs 27, 325-349.

Brokaw, N., 1998. Fragments past, present and future. Trends in Ecology and Evolution 13, 382-383.

Brown, C.A., 2001. A comparison of several methods of assessing river condition using benthic macroinvertebrate assemblages. African Journal of Aquatic Science 26, 135-147.

Brown, K.S. Jr., 1991. Conservation of insects and their habitats: insects as indicators. In The conservation of insects and their habitats, eds. N.M. Collins and J.A. Thomas, pp. 350-404. Academic Press, London.

Brown, V.K., Southwood, T.R.E., 1983. Trophic diversity, niche breadth and generation times of exopterygote insects in a secondary succession. Oecologia 56, 220-225.

Bulánková, E., 1997. Dragonflies (Odonata) as bioindicators of environmental quality. Biologia 52(2), 177-180.

Bunn, S.E., 1988. Processing of leaf litter in a northern jarrah forest stream, Western Australia: I. Seasonal differences. Hydrobiologia 162, 211-223.

Bunn, S.E., Boon, P.I., 1993. What sources of organic carbon drive food webs in billabongs? A study based on stable isotope analysis. Oecologia 96, 85-94.

Bunn, S.E., Davies, P.M., Kellaway, D.M., 1997. Contributions of sugar cane and invasive pasture grass to the aquatic food web of a tropical lowland stream. Marine Freshwater Research 48, 173-179.

Bunn, S.E., Davies, P.M., Mosisch, T.D., 1999. Ecosystem measures of river health and their response to riparian and catchment degradation. Freshwater Biology, 41, 333-345.

Campbell, I.C., 1994. The challenges of stream habitat assessment. In Classification of Rivers and Environmental Health Indicators, ed. M.C. Uys, WRC Report No. TT 63/94, pp. 205-216. Water Research Commission, Pretoria.

Campbell, I.C., Doeg, T.J., 1989. Impact of timber harvesting and production on streams. Australian Journal of Marine and Freshwater Research 40, 519-539.

Canhoto, C., Graca, M.A.S., 1995. Food value of introduced *Eucalyptus* leaves for a Mediterranean stream detritivore: *Tipula lateralis*. Freshwater Biology 34, 209-214.

Cao, Y., Bark, A.W., Williams, W.P., 1997. Analysing benthic macroinvertebrate community changes along a pollution gradient: a framework for the development of biotic indices. Water Research 31(4), 884-892.

Carlisle, D.M., Clements, W.H., 1999. Sensitivity and variability of metrics used in biological assessments of running water. Environmental Toxicology and Chemistry 18 (2): 285-291.

Chessman, B.C., 1994. The use of macroinvertebrates for the rapid biological assessment of streams in the Sydney Region, New South Wales, Australia. In Uys MC (ed.) Classification of river and environmental health indicators. Proceedings of a joint South Africa/Australia workshop. February 7-14 1994, Cape Town, South Africa. Water Research Commission Report No. TT63/94. Water Research Commission, Pretoria, South Africa.

Chessman, B.C., 1995. Rapid assessment of rivers using macroinvertebrates: a procedure based on habitat-specific sampling, family level identification and a biotic index. Australian Journal of Ecology 20, 122-129.

Chovanec, A., Waringer, J., 2001. Ecological integrity of river-floodplain systems – assessment by dragonfly surveys (Insecta: Odonata). Regulated Rivers Research and Management 17, 493-507.

Chutter, F.M., 1972. An empirical biotic index of the quality of water in South African streams and rivers. Water Research 6, 19-30.

Chutter F.M., 1994. The rapid biological assessment of streams and river water quality by means of macroinvertebrate communities in South Africa. In Classification of Rivers and Environmental Health Indicators, ed. M.C. Uys, WRC Report No. TT 63/94, pp. 217-234. Water Research Commission, Pretoria.

Chutter F.M., 1998. Research on the Rapid Biological Assessment of Water Quality Impacts in Streams and Rivers. Report to the Water Research Commission, Pretoria. WRC Report No. 422/1/98.

Clark, T.E., Samways, M.J., 1996. Dragonflies (Odonata) as indicators of biotope quality in the Kruger National Park, South Africa. Journal of Applied Ecology 33, 1001-1012.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18, 117-143.

Clarke, K.R., Warwick, R.M., 2001. Change in marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd edn. PRIMER-E Ltd, Plymouth.

Connell, J. H., 1978. Diversity in tropical rainforests and coral reefs. *Science* 199, 1302-1310.

Corbet, P.S., 1999. Dragonflies: Behaviour and Ecology of Odonata. Harley Books, Colchester, United Kingdom.

Cummins, K.W., Wilzbach, M.W., Gates, D.M., Perry, J.B., Taliaferro, W.B., 1989. Shredders and riparian vegetations. BioScience 39, 24-30.

Dallas, H.F., 1995. An Evaluation of SASS (South African Scoring System) as a Tool for the Rapid Bioassessment of Water Quality. MSc Thesis, Department of Zoology, University of Cape Town, Cape Town, South Africa.

Dallas, H.F., 1997. A preliminary evaluation of aspects of SASS (South African Scoring System) for the rapid bioassessment of water quality in rivers, with particular reference to the incorporation of SASS in a national biomonitoring programme. Southern African Journal of Aquatic Sciences 23, 79-94.

Dallas, H.F., 2000. Ecological Reference Condition Project: Field Manual. General Information, Catchment Condition, Invertebrates and Water Chemistry. NAEBP Report Series No. 10. Institute for Water Quality Studies, Department of Water Affairs and Forestry, Pretoria, South Africa.

Dallas, H.F., 2002. Spatial and Temporal Heterogeneity in Lotic Systems: Implications for Defining Reference Conditions for Macroinvertebrates. PhD Thesis, Department of Zoology, University of Cape Town, Cape Town, South Africa.

Dallas, H.F., Day, D.E., 1993. The effect of water quality variables on riverine ecosystems: a review. WRC Report No. TT 61/93. Water Research Commission, Pretoria.

Dallas, H.F., Day, D.E., Musibono, D.E., Day, E.G., 1998. Water Quality for Aquatic Systems: Tools for Evaluating Regional Guidelines. WRC Report No. 626/1/98. Water Research Commission, Pretoria

Dallas, H.F., Day, D.E., Reynolds, E.G., 1994. The Effects of Water Quality Variables on Riverine Biotas. WRC Report No. 626/1/98. Water Research Commission, Pretoria

Davies, P.M., 1994. Ecosystem Processes: a direct assessment of river health. In Classification of Rivers and Environmental Health Indicators, Proceedings of a joint South African-Australian workshop, February 7-14, Cape Town, South Africa, ed. M.C. Uys, WRC Report No. TT63/94, pp. 119-128. Water Research Commission, Pretoria.

Davies, B., Day, J., 1998. Vanishing Waters. University of Cape Town Press, Cape Town.

Day, J.A., King, J.M., 1995. Geographical patterns, and their origins, in the dominance of major ions in South African rivers. South African Journal of Science 91, 299-306.

De Moor, F.C., Scott, K.M.F., 2003. Chapter 5: Trichoptera. In Freshwater Invertebrates of Southern Africa Volume 8: Insecta II; Hemiptera, Megaloptera, Neuroptera, Trichoptera and Lepidoptera, eds. I.J. de Moor, J.A. Day, F.C. de Moor, WRC Report No. TT 214/03, pp. 84-169. Water Research Commission, Pretoria.

Dickens, C.W.S., Graham, P.M., 1998. Biomonitoring for effective management of wastewater discharges and the health of the river environment. Aquatic Ecosystem Health and Management 1, 199-217.

Dickens, C.W.S., Graham, P.M., 2002. The South African Scoring System (SASS) version 5 rapid bioassessment system for rivers. African Journal of Aquatic Science 27, 1-10.

Donnelly, D., Giliomee, J.H., 1985. Community structure of epigaeic ants in a pine plantation and newly burnt fynbos. Journal of the entomological Society of southern Africa 48, 259-265.

Downes, P.W., Skinner, K.S., Kondolf, G.M., 2002. Rivers and streams. In Handbook of Ecological Restoration. Volume 2. Restoration in Practice, eds. M.R. Perrow, A.J. Davy, pp. 267-295. Cambridge University Press, Cambridge.

DWAF (Department of Water Affairs and Forestry), 1999. Water Resources Protection Policy Implementation: Resource Directed Measures for Protection of Water Resources, version 1.0. Department of Water Affairs and Forestry, Pretoria. www.dwaf.pwv.gov.za

Dufrêne, M., Legendre, P., 1997. Species assemblages an indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67(3), 345-366.

Fletcher, A.R., 1979. Effects of *Salmo trutter* on *Galaxias olidus* and macroinvertebrates in stream communities. MSc Thesis, Monash University, Melbourne.

Fry, R., Lonsdale, D., 1991. Introduction. In Habitat Conservation for Insects - a Neglected Green Issues, eds. R. Fry, D. Lonsdale, pp. 1-14. The Amateur Entomologist 21, The Amateur Entomologists' Society, Essex.

Furse, M.T., Moss, D., Wright, J.F., Armitage, P.D., 1984. The influences of seasonal and taxonomic factors on the ordination and classification of running water sites and on the prediction of macro-invertebrate communities. Freshwater Biology 14, 257-280.

Gasith, A., Resh, V.H., 1999. Streams in Mediterranean Climate Regions: Abiotic influences and biotic responses to predictable seasonal events. Annual Review of Ecological Systematics 30, 51-81.

Gerritson, J., Barbour, M.T., King, J., 2000. Apples, oranges and ecoregions: on determining pattern in aquatic assemblages. Journal of the North American Benthological Society 19(3), 487-496.

Gore, J.A., 1985. Restoration of Rivers and Streams. Butterworth Publications, Boston.

Gratwicke, B., 1998. The effect of season on a biotic water quality index: a case study of the Yellow Jacket and Mazowe Rivers, Zimbabwe. South African Journal of Aquatic Science 24(1), 24-35.

Guerold, F., 2000. Influence of taxonomic determination level of several community indices. Water Research 34(2), 487-492.

Haddad, N., 2000. Corridor length and patch colonization by a butterfly, *Junonia coenia.* Conservation Biology 14(3), 738-745.

Harrison, A.D., 1965. Geographical distribution of riverine invertebrates in southern Africa. Archiv für Hydrobiologie 61, 387-394.

Harrison, A.D., Agnew, J.D., 1962. The distribution of invertebrates endemic to acid streams in the Western and Southern Cape Province. Annals of the Cape Provincial Museums II, CSIR Reprint No. RW 121, Pretoria, South Africa.

Hellawell, J.M., 1991. Development of a rationale for monitoring. In Monitoring for Conservation and Ecology, ed. B. Goldsmith, pp. 3-14. Chapman and Hall, London.

Henderson, J.E., 1986. Environmental designs for stream bank protection projects. Water Resources Bulletin 22(4), 549-558.

Holmes, P.M., Dallas, H., Phillips, T., 1987. Control of *Acacia saligna* in the SW Cape – are the clearing treatments effective? Veld and Flora 73(3): 98-100.

Holmes, P.M., Marais, C., 2000. Impacts of alien plant clearance on vegetation in the mountain catchments of the western Cape. South African Forestry Journal 189, 113-117.

Holmes, P.M., Richardson, D.M., 1999. Protocols for restoration based on knowledge of recruitment dynamics, community structure and ecosystem function: perspectives from South African fynbos. Restoration Ecology 7, 215-231.

Holmes, P.M., Richardson, D.M., van Wilgen, B.W., Gelderblom, C., 2000. Recovery of South African fynbos vegetation following alien woody plant clearing and fire: implications for restoration. Austral Ecology 25, 631-639.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54, 187-211.

Jenkins, D.W., 1971. Global biological monitoring. In Man's Impact on Terrestrial and Oceanic Ecosystems, eds. W.H. Matthews, F.E. Smith, E.D. Goldberg, pp. 351-370. MIT, Cambridge, Massachusetts.

Johnson, R.K., Wiederholm, T., Rosenburg, D.M., 1993. Freshwater biomonitoring using individual organsims, populaions and species assemblages of benthic macroinvertebrates. In Freshwater Biomonitoring and Benthic Macroinvertebrates, eds. D.M. Rosenberg, V.H. Resh, pp. 40-158. Chapman and Hall, New York.

Kemper, N.P., 2001. RVI Riparian Vegetation Index. WRC Report No. 850/3/01. Water Research Commission, Pretoria.

King, J.M., 1981. The distribution of invertebrate communities in a small South African river. Hydrobiologia 83, 43-65.

King, J.M., 1982. An Ecological Study of the Macroinvertebrate fauna of the Eerste River, Western Cape Province, South Africa. PhD Thesis, Department of Zoology, University of Cape Town, Cape Town, South Africa.

King, J.M., 1983. Abundance, biomass and diversity of benthic macro-invertebrates in a Western Cape river, South Africa. Transactions of the Royal Society of South Africa 45(1), 11-34.

King, J.M., Scheepers, A.C.T., Fisher, R.C., Reinecke, M.K., Smith, L.B., 2003. River rehabilitation: literature review, case studies and emerging principles. WRC Report No. 1161/1/03. Water Research Commission, Pretoria.

King, J.M, Schael, D.M., 2001. Assessing the ecological relevance of a spatially-nested geomorphological hierarchy for river management. WRC Report No. 754/1/01. Water Research Commission, Pretoria.

Kinvig, R.G., Samways, M.J., 2000. Conserving dragonflies (Odonata) along streams running through commercial forestry. Odonatologica 29(3), 195-208.

Kondolf, G.M., 1998. Lessons learned from river restoration projects in California. Aquatic Conservation: Marine and Freshwater Ecosystems 8, 39-52.

Kondolf, G.M., Micheli, E.R., 1995. Evaluating stream restoration projects. Environmental Management 19(1), 1-15.

Lenat, D.R., 1988. Water quality assessment of streams using a qualitative assessment method for benthic macroinvertebrates. Journal of the North American Benthological Society 7, 222-223.

Lenat, D.R., Crawford, J.K., 1994. Effects of land use on water quality and aquatic biota of three North Carolina Piedmont streams. Hydrobiologia 294, 185-199.

Levitt, M., 1997. Putting Fynbos back. Veld and Flora 83(3), 81-83.

Luedtke, R.J., Brusven, M.A., 1976. Effects of sand sedimentation on colonisation of stream insects. Journal of Fisheries Research, Canada 33, 1881-1886.

Mac Arthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Malan, H.L., Day, J.A., 2002. Linking discharge, water quality and biotic response in rivers: a literature review. WRC Report No. 956/2/02. Water Research Commission, Pretoria.

Manly, B.F.J., 1990. Randomization and Monte Carlo methods in biology. Chapman and Hall, London.

Maridet, L., Philippe, M, Wasson, J.G., Mathieu, J., 1996. Spatial and temporal distribution of macroinvertebrates and trophic variables within the bed sediment of three streams differing by their morphology and riparian vegetation. Archiv für Hydrobiologie 136(1), 41-64.

Maridet, L., Wasson, J.G., Philippe, M., Amoros, C., Naiman, R.J., 1998. Trophic structure of three streams with contrasting riparian vegetation and geomorphology. Archiv für Hydrobiologie 144, 61-85.

McCann, K., Lindley, D., 1998. Rehabilitation of eroded riverbanks and wetlands. Farmers Weekly 86-88

McGeoch, M.A., 1998. The selection, testing and application of terrestrial insects as bioindicators. Biological Reviews 73, 181-201.

McGeoch, M.A., 2002. Bioindicators. In Encyclopaedia of Envirometrics, eds. A.H. El-Shaarawi, W.W. Piegorsch, pp. 186-189. John Wiley, Chichester.

McGeoch, M.A., van Rensburg, B.J., Botes, A., 2002. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. Journal of Applied Ecology 39, 661-672.

McMillan, P.H., 1998. An Integrated Habitat Assessment System (IHAS v2), for the rapid biological assessment of rivers and streams. A CSIR Research Project, number ENV-P-I 98 132 for the Water Resources Management Programme, CSIR, Pretoria, South Africa.

McNeely, J.A., Gadgil, M., Leuèque, C., Padoch, C., Redford, K., 1995. Human influences on biodiversity. In Global Biodiversity Assessment, ed. V.H. Heywood, pp. 711-822. Cambridge University press, Cambridge.

Morely, S.A., Karr, J.R., 2002. Assessing and restoring the health of urban streams in the Puget Sound Basin. Conservation Biology 16(6), 1498-1509.

Moss, D., Furse, M.T., Wright, J.F., Armitage, P.D., 1987. The prediction of the macroinvertebrate fauna of unpolluted running-water sites in Great Britain using environmental data. Freshwater Biology 17, 41-52.

Muotka, T., Laasonen, P., 2002. Ecosystem recovery in restored headwater streams: the role of enhanced leaf retention. Journal of Applied Ecology 39, 145-156.

Myers, N., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853-858.

New, T.R., 1993. Effects of exotic species on Australian native species. In Perspectives on Insect Conservation, eds. K.J. Gaston, T.R. New, M.J. Samways, pp. 155-170. Intercept, Andover.

Noss, R.F., 1991. Landscape connectivity: different functions at different scales. In Landscape Linkages and Biodiversity, pp. 27-39. Island Press, Washington.

Ormerod, S.J., Wade, K.R., Gee, A.S., 1987. Macrofloral assemblages in upland Welsh streams in relation to acidity, and their importance to invertebrates. Freshwater Biology 18, 545-557.

Osborn, R., Samways, M.J., 1996. Determinants of adult dragonfly assemblage patterns at new ponds in South Africa. Odonatologica 25(1), 49-58.

Palmer, M.W., 1993. Putting the things in even better order: the advantages of canonical correspondence analysis. Ecology 74(8), 2215-2230.

Phiri, C., 2000. An assessment of the health of two rivers within Harare, Zimbabwe, on the basis of macroinvertebrate community structure and selected physico-chemical variables. African Journal of Aquatic science 25, 134-145.

Pienaar, E., Boucher, C., Brown, C., 2003. Distribution of *Acacia mearnsii* seed along depth and lateral profiles in natural and infested stands along selected rivers in the Breede River system. Unpublished report. Department of Botany, University of Stellenbosch, South Africa.

Quinn, J.M., Cooper, A.B., Davies-Colley, R.J., Rutherford, J.C., Williamson, R.B., 1997. Land use effects on habitat, water quality, periphyton and benthic invertebrates in Waikato, New Zealand, hill-country streams. New Zealand Journal of Marine and Freshwater Research 31(5), 579-597.

Resh, V.H., McElravy, E.P., 1993. Contemporary quantitative approaches to biomonitoring using benthic macroinvertebrates. In Freshwater Biomonitoring and Benthic Macroinvertebrates, eds. D.M. Rosenberg, V.H. Resh, pp. 160-194. Chapman and Hall, New York.

Resh, V.H., Jackson, J.K., 1993. Rapid assessment approaches to biomonitoring using benthic macroinvertebrates. In Freshwater Biomonitoring and Benthic Macroinvertebrates, eds. D.M. Rosenberg, V.H. Resh, pp. 195-203. Chapman and Hall, New York.

Richardson, D.M., van Wilgen, B.W., 2004. Invasive alien plants in South Africa: how well do we understand the ecological impacts? South African Journal of Science 100, 45-52.

Rosenberg, D.K., Noon, B.R., Meslow, E.C., 1997. Biological corridors: form function and efficacy. BioScience 47(10), 677-687.

Rosenberg, D.M., Resh, V.H., (eds) 1993. Freshwater Biomonitoring and Freshwater Macroinvertebrates. Chapman and Hall, New York, London.

Roque, F.O., Trivinho-Strixino, S., Strixino, G., Agostinho, R.C., Fogo, J.C., 2003. Benthic macroinvertebrates in streams of the Jaragua State Park (Southeast of Brazil) considering multiple spatial scales. Journal of Insect Conservation 7, 63-72.

Roux, D.J., 1997. National Aquatic Ecosystem Biomonitoring Programme: Overview of the Design Process and Guidelines for Implementation. NAEBP Report Series No. 6. Department of Water Affairs and Forestry, Pretoria.

Rutherfurd, I.D., Abernethy, B., Prosser, I., 2000b. Stream erosion. In Riparian Land Management Technical Guidelines, volume one: Principles of Sound Management, eds. S. Lovett, P. Price. Land and Water Resources Research and Development Corporation, Canberra, Australia.

Rutherfurd, I.D., Jerie, K., Marsh, N., 2000a. A rehabilitation manual for Australian streams, Volumes 1 and 2. Cooperative Research Centre for Catchment Hydrology, and Land and Water Resources Research and development Corporation. Canberra, Australia. Accessible at www.rivers.gov.au

Rutherfurd, I.D., Ladson, A., Tilleard, J., Stewardson, M., Ewing, S., Brierley, G., Fryirs, K., 1998. Research and development needs for river restoration in Australia. Report to the National River Health Program Management Committee of the Land and Water Resources Research and Development Corporation, Canberra, Australia.

Rutt, G.P., Weatherley, N.S., Ormerod, S.J., 1989. Microhabitat availability in Welsh moorland and forest streams as a determinant of macroinvertebrate distribution. Freshwater Biology 22, 247-261.

Rutt, G.P., Weatherley, N.S., Ormerod, S.J., 1990. Relationship between the physicochemistry and macroinvertebrates of British upland streams: the development of a modelling and indicator system for predicting fauna and detecting acidity. Freshwater Biology 24, 463-480.

Sahlén, G., Ekestubbe, K., 2001. Identification of dragonflies (Odonata) as indicators of general species richness in boreal forest lakes. Biodiversity and Conservation 10, 673-690.

Samways, M.J., 1993a. A spatial and process sub-regional framework for insect and biodiversity conservation research and management. In Perspectives on Insect Conservation, eds. K.J. Gaston, T.R. New, M.J. Samways, pp. 1-28. Intercept, Andover.

Samways, M.J., 1993b. Dragonflies (Odonata) in taxic overlays and biodiversity conservation. In Perspectives on Insect Conservation, eds. K.J. Gaston, T.R. New, M.J. Samways, pp. 111-124. Intercept, Andover.

Samways, M.J., 1994. Insect Conservation Biology. Chapman and Hall, London.

Samways, M.J., Caldwell, P.M., Osborn, R., 1996. Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. Agriculture, Ecosystems and Environment 59, 19-32.

Samways, M.J., Wilmot, B.C., 2003. Chapter 3: Odonata. In Freshwater Invertebrates of Southern Africa Volume 7: Insecta I; Ephemeroptera, Odonata and Plecoptera. ed I.J. de Moor, J.A. Day, F.C. de Moor, WRC Report No. TT 207/03, pp. 160-200. Water Research Commission, Pretoria.

Saunders, J.J., Meeuwig, J.J., Vincent, A.C.J., 2002. Freshwater protected areas: strategies for conservation. Conservation Biology 16(1), 30-41.

Schofield, K., Townsend, C.R., Hildrew, A.G., 1988. Predation and the prey community of a headwater stream. Freshwater biology 20, 85-95.

Schmidt, E., 1985. Habitat inventariszation, characterization and bioindication by a "representative spectrum of Odonata species". Odonatologica 14(2), 127-133.

Scott, D.F., Versfeld, D.B., Lesch, W., 1998. Erosion and sediment yield in relation to afforestation and fire in the mountains of the Western Cape Province, South Africa. South African Geographical Journal 80(1), 52-59.

Simberloff, D.S. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biological Conservation 83, 247-257.

Stevens, D.M., Picker, M.D., 1999. A revision of *Aphanicercella* Tillyard (Plecoptera: Notonemouridae) including the *A. barnardi* (Tillyard) species-complex. African Entomology 7, 197-209.

Stevens, D.M., Picker, M.D., 2003. Chapter 4: Plecoptera. In Freshwater Invertebrates of Southern Africa Volume 7: Insecta I; Ephemeroptera, Odonata and Plecoptera. ed I.J. de Moor, J.A. Day, F.C. de Moor, WRC Report No. TT 207/03, pp. 213-263. Water Research Commission, Pretoria.

Stewart, D.A.B., Samways, M.J., 1998 Conserving dragonfly (Odonata) assemblages relative to river dynamics in an African savanna game reserve. Conservation Biology 12(3), 683-692.

Stewart-Oaten, A., Bence, J.R., Osenberg, C.W., 1992. Assessing the effects of unreplicated perturbations: no simple solutions. Ecology 73(4), 1396-1404.

Steytler, N.S., Samways, M.J., 1995. Biotope selection by adult male dragonflies (Odonata) at an artificial lake created for insect conservation in South Africa. Biological Conservation 72, 381-386.

Stork, N.E., Samways, M.J., 1995. Inventorying and monitoring of biodiversity. In Global Biodiversity Assessment, ed. V.H. Heywood, pp. 453-544. Cambridge University Press, Cambridge.

Stubbs, A., 1991. The management of aquatic habitats. In Habitat Conservation for Insects - a Neglected Green Issues, eds. R. Fry, D. Lonsdale, pp. 159-175. The Amateur Entomologist 21, The Amateur Entomologists' Society, Essex.

Stubbs, A., Warren, P., 1991. Aquatic water margin habitats; ecological principles and problems. In Habitat Conservation for Insects – a Neglected Green Issues, eds. R. Fry, D. Lonsdale, pp. 151-158. The Amateur Entomologist 21, The Amateur Entomologists' Society, Essex.

Ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67, 1167-1179.

Ter Braak, C.F.J., 1988. Chapter 5. Ordination. In Data Analysis in Community Ecology, ed. R.H.G. Jongman, C.J.F. ter Braak, O.F.R. van Tongeren, pp. 91-173. Cambridge University Press, Cambridge.

Ter Braak, C.F.J., 1992. Permutation versus bootstrap significance tests in multiple regression and ANOVA. In Bootstrapping and related techniques, ed. K.H. Jökel, G. Rothe, W. Sendler, pp. 79-86. Springer Verlag, Berlin.

Ter Braak, C.J.F., Smilauer, P., 2002. CANOCO reference manual and user's guide to Canoco for Windows: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, New York.

Ter Braak, C.J.F., Verdonschot, P.F.M., 1995. Canonical correspondence analysis and related methods in aquatic ecology. Aquatic Sciences 57(3), 153-185.

Underwood, A.J., 1998. Experiments in Ecology. Cambridge University Press, Cambridge.

Usher, M.B., 1988. Biological invasions of nature reserves: a search for generalizations. Biological Conservation 44, 119-135.

Usher, M.B., Jefferson, R.G., 1993. Creating new and successional habitats for arthropods. In The Conservation of Insects and their Habitats, eds. N.M. Collins, J.A.Thomas, pp. 263-293. Academic Press, London.

Uys, A.C., 2003. Development of river rehabilitation in Australia: lessons for South Africa. WRC Report No. KV 144/03. Water Research Commission, Pretoria.

Uys, M.U., Goetsch, M.A., O'Keeffe, J.H., 1996. Ecological Indicators, a Review and Recommendations. National Biomonitoring Programme for Riverine Ecosystems Report Series No. 4. Institute for Water Quality Studies, Department of Water Affairs and Forestry, Pretoria, South Africa.

Vane-Wright, R.I., 1993. Systematics and the conservation of biodiversity: global, national and local perspectives. In Perspectives on Insect Conservation, eds. K.J. Gaston, T.R. New, M.J. Samways, pp. 197-212. Intercept, Andover.

Van Rensburg, B.J., McGeoch, M.A., Chown, S.L., Van Jaarsveld, A.S., 1999. Conservation of heterogeneity among dung beetles in the Maputoland Centre of Endemism, South Africa. Biological Conservation 88, 145-153.

Vegter, J.R., 1995. Geology map of South Africa with simplified lithostratigraphy for geohydrological use. Water Research Commission TT 74/95, Pretoria, South Africa.

Verdonschot, P.F.M., ter Braak, C.J.F., 1994. An experimental manipulation of oligochaete communities in mesocosms treated with chlorpyrifos or nutrient additions: multivariate analysis with Monte Carlo permutation tests. Hydrobiologia 278, 251-266.

Vuori, K. Joensuu, I. 1996. Impact of forest drainage on the macroinvertebrates of a small boreal headwater stream: do buffer zones protect lotic biodiversity? Biological Conservation 77, 87-95.

Wallace, J.B., Grubaugh, J.W., Whiles, M.R., 1996. Biotic indices and stream ecosystem processes: results from an experimental study. Ecological applications 6(1), 140-151.

Warwick, R.M., 1993. Environmental impact studies on marine communities: pragmatic considerations. Australian Journal of Ecology 18, 63-80.

Weatherley, N.S., Rutt, G.P., Ormerod, S.J., 1989. Densities of macroinvertebrates in upland Welsh streams of different acidity and land use. Archiv für Hydrobiologie 115(3), 417-431.

Williams, K.S., 1997. Terrestrial arthropods as ecological indicators of habitat restoration in southwestern North America. In Restoration Ecology and Sustainable Development, eds. K.M. Urbanska, N.R. Webb, P.J. Edwards, pp. 238-258. Cambridge University Press, Cambridge.

Willson, J.D., Dorcas, M.E., 2003. Effects of habitat disturbance on stream salamanders: implications for buffer zones and watershed management. Conservation Biology 17(3), 763-771.

Wilson, D.S., Yoshimura, J., 1994 On the coexistence of specialists and generalists. The American Naturalist 144, 692-707.

Wishart, M.J., Davies, B.R., Stewart, B.A., Hughes, J.M., 2003. Examining Catchments as Functional Units for the Conservation of Riverine Biota and Maintenance of Biodiversity. WRC Report No. 975/1/02. Water Research Commission, Pretoria.

Wishart, M.J., Day, J.A., 2001. Endemism in the freshwater fauna of the South-Western Cape, South Africa. Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie 2001.

WRI/IUCN/UNEP, 1992. Global Biodiversity Strategy: Guidelines for Action to Save, Study and Use Earth's Biotic Wealth Sustainably and Equitably. WRI/IUCN/UNEP, World Resources Institute, Washington DC.

Wright, I.A., Chessman, B.C., Fairweather, P.G., Benson, LJ., 1995. Measuring impacts of sewage effluent on the macroinvertebrate community of an upland stream: the effect of different levels of taxonomic resolution and quantification. Australian Journal of Ecology 20, 142-149.

Wright, J.F., 1995. Development and use of a system for predicting the macroinvertebrate fauna in flowing waters. Australian Journal of Ecology 20, 181-197.

Wright, J.F., Moss, D. Armitage, P.D., Furse, M.T., 1984. A preliminary classification of running-water sites in Great Britain based on macro-invertebrate species and the prediction of community type using environmental data. Freshwater Biology 14, 221-256.

Wright, M.G., 1993. Insect conservation in the African Cape Fynbos, with special reference to endophagous insects. In Perspectives on Insect Conservation, eds. K.J. Gaston, T.R. New, M.J. Samways, pp. 97-110. Intercept, Andover.

Zavaleta, E.S., Hobbs, R.J., Mooney, H.A., 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology and Evolution 16(8), 454-459.

Zwick, P., 1992. Stream habitat fragmentation - a threat to biodiversity. Biodiversity and Conservation 1, 80-97.

Chapter 4

Final Discussion

The effect of alien disturbance along rivers in the Western Cape was determined in two parallel studies, using benthic macroinvertebrates on the one hand, and aerial odonates on the other. No attempt was made to correlate the findings from the two studies. However, a number of biological and biogeographical trends were evident in both. These are summarised below.

1. While alien invasion had a negative effect on richness and abundance, removal of alien trees appeared to initiate some measure of recovery, not only in terms of overall abundance and richness, but also in terms of faunal composition and distribution patterns. This is encouraging for the Working for Water Programme and validates the need for ongoing clearing.

2. However, biodiversity management needs to consider processes, not just number of species (Samways, 1994). For instance, rare, endemic species are likely to be most important for conservation and may be useful as indicators, but they are also likely to be most vulnerable to disturbance (Samways, 1993). In this study, endemic taxa were harmed by either alien invasion or alien clearing, or by both. Moreover, the main beneficiaries of alien clearing were the more tolerant, widespread, eurytopic taxa that benefited from the abundance of marginal macrophytes in sunlit, cleared sites. Recovery of endemic and sensitive taxa, on the other hand, is somewhat delayed and often only occurs after the recovery of indigenous *Prionium*, fynbos and trees. In terms of biodiversity objectives, this is cause for concern as rare, endemic taxa, such as *Chlorolestes umbratus*, may take years to recover. Clearly, alien disturbance affects the quantity and quality of marginal plant biotopes available to endemic taxa and it is therefore strongly recommended that Working for Water implement effective

measures to maintain and restore indigenous marginal vegetation, thus providing for the habitat requirements of these taxa. Recommendations for doing this are given in Table 1.

3. Alien disturbance also affected water quality. Shaded, alien sites had relatively low temperatures, while sunlit, cleared sites had the highest temperatures and lowest oxygen levels. The exposed banks of alien sites experienced erosion, which raised levels of suspended solids, increased conductivity and added to sandy substrates. However, removal of alien vegetation clearly exacerbated this effect, so that cleared sites had the highest suspended solid concentrations and conductivities and the sandiest substrates. This, together with the low oxygen levels in warm, cleared sites, may have been limiting for certain sensitive and endemic taxa. Therefore, for effective management of biodiversity, Working for Water needs to address both water quality (e.g. erosion and temperature) and habitat quality (indigenous marginal vegetation) issues. Recommendations are given in Table 1.

4. All aerial Odonata were negatively affected by alien invasion because of the absence of understorey plants and the resulting lack of suitable perch and oviposition sites. Moreover, all odonates appeared to benefit, at least in the long term, by alien removal. Amongst aquatic macroinvertebrates, on the other hand, responses to invasion and clearing were highly variable, particularly amongst the Trichoptera. While several invertebrate taxa were clearly sensitive to alien invasion, others appeared to be tolerant of invasion and may even benefit from it. In these cases, alien invasion may have modified water quality conditions (e.g. temperature and oxygen), habitats (e.g. availability of wood debris for case-building Trichoptera) or food availability (e.g. plant debris for shredders or diatoms for scrapers) that may have benefited certain taxa. Similarly, while some taxa, most notably larval odonates, benefited from alien clearing, others were sensitive to the changes in water quality, food or habitats that accompanied alien clearing.

5. A comparison of the adult and larval Odonata, sampled by visual observations and SASS5 respectively, showed a considerable discrepancy between the adult and larval taxa present along and in the river at any one time. No Platycnemidae, Synlestidae or Protoneuridae larvae were sampled in any sites, while adults within these families (*Allocnemis leucosticta*, *C. umbratus* and *Elattoneura frenulata*) were fairly common in natural sites, at least along the Molenaars River. It is possible, therefore, that the standardised SASS methodology does not sample all taxa with equal efficiency. For the Odonata, at least, SASS appears inadequate for sampling all families and this places some doubt on its reliability as a bioassessment method. The consistency of the method is also questionable because the chance sampling of only one individual platycnemid, which scores 10 SASS points, would have a marked effect on the final SASS score. Because these species are endemic to the Cape, and *C. umbratus* is rare, it would be important to investigate the reason for their absence from SASS samples, as seasonal emergence patterns or disturbance effects may also be involved.

6. Larvae, being aquatic and present throughout the year, are probably more useful for detecting changes to both habitats and physico-chemical conditions in aquatic systems. However, because of the inter-relatedness of environmental variables, it is difficult to identify causal relationships. Therefore, while SASS is useful for baseline studies to detect overall changes in river health, it should be used in taxic overlays with other taxa, including endemic and rare species, to provide a more complete picture of ecological integrity. Moreover, SASS should not be over-interpreted or linked to specific causes, such as alien disturbance. For this, quantitative methods are required. For example, indicator taxa or the proportion of endemic to widespread taxa may be used to answer specific questions about alien disturbance that can inform biodiversity management decisions.

7. Because water quality assessments, such as SASS, lack consistency and precision, the response of fauna to the quality and quantity of marginal or substrate habitats may be a more

reliable assessment of alien disturbance. This is a further reason to complement SASS with quantitative community studies. Adult Odonata, in particular, were effective at classifying marginal plant biotopes, while larval odonates showed some potential to do the same, if effectively sampled. More effective sampling of odonate larvae could be useful to complement these aerial responses with aquatic responses, thus giving a more complete picture of both biotope quality and water quality.

8. Benthic macroinvertebrate distribution patterns confirmed the findings of King and Schael (2001) that each river has its own signiature fauna that respond differently to alien disturbance. Amongst aerial odonates, however, between-river differences were far less evident, with considerable overlap occurring between rivers and catchments. The greater dispersal capabilities of Odonata is the likely explanation for this, which agrees with the findings of Wishart *et al.* (2003) who observed that the degree of genetic variation in a population reflected the dispersal characteristics of each species. Poor dispersers, such as the plecopteran, *Aphanicerca capensis*, displayed high degrees of population structure in terms of their genetics in each catchment, while good dispersers, such as the dragonfly, *Aeshna subpupillata*, displayed little genetic variation between catchment populations. This suggests that good dispersers are able to move freely between catchments. This has implications for the management of catchments according to biodiversity criteria (see Table 1).

9. Alien disturbance appeared to affect the seasonal activity patterns of adult Odonata and it is possible that the temperature and insolation changes that accompany alien disturbance have far-reaching effects on life cycles patterns, emergence times, growth and survival of all aquatic invertebrates. The effect this has on endemic taxa should be determined.

10. It is recommended that alien clearing programmes change their emphasis from pure eradication to a more integrated approach that incorporates restoration and biodiversity

conservation goals. Management recommendations relevant to both studies are summarised in Table 1. Further research into the recovery rates under different disturbance scenarios would help to fine-tune these recommendations.

Conclusion

While alien clearing programmes are doing much to initiate the recovery of aquatic fauna in terms of abundance and richness, the restoration of ecosystem function and the achievement of biodiversity objectives, remain unrealised. To achieve these goals, the habitat and water quality needs of sensitive, endemic taxa need to be addressed by careful planning, prioritisation and active restoration, together with long-term monitoring and assessment using a range of assessment methods.

References

King, J.M, Schael, D.M., 2001. Assessing the ecological relevance of a spatially-nested geomorphological hierarchy for river management. WRC Report No. 754/1/01. Water Research Commission, Pretoria.

Samways, M.J., 1993. Dragonflies (Odonata) in taxic overlays and biodiversity conservation. In Perspectives on Insect Conservation, eds. K.J. Gaston, T.R. New, M.J. Samways, pp. 111-124. Intercept, Andover.

Samways, M.J., 1994. Insect Conservation Biology. Chapman and Hall, London.

Wishart, M.J., Day, J.A., 2001. Endemism in the freshwater fauna of the South-Western Cape, South Africa. Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie 2001.

Table 1

Management recommendations for alien clearing, summarised for aerial odonates and aquatic macroinvertebrates. To achieve functional (and, therefore, biodiversity) endpoints, all three steps (A – C) need to be incorporated into a process of planning, implementation and assessment. The restoration technology that is used should be appropriate for the specific restoration scenario.

	Aerial Odonata	**Benthic macroinvertebrates**
A. RESTORE		
Water quality	1. Reduce erosion of cleared banks using bank stabilisation methods: • cultivate and maintain indigenous plants • use bio-engineering methods or natural structures • use fell-remove-burn methods and reduce fire intensities	1. Reduce erosion of cleared banks using bank stabilisation methods: • cultivate and maintain indigenous plants • use bio-engineering methods or natural structures • use fell-remove-burn methods and reduce fire intensities 2. Provide shade to regulate temperature and oxygen: • cultivate and maintain indigenous plants and seed banks • prioritise less-dense areas with existing indigenous plants for ease of recovery • use fell-remove-burn methods to reduce fire intensities
Habitats	1. Maintain and restore indigenous plant biotopes, thus maintaining the endemic species associated with them. • Cultivate and maintain indigenous plants and seed banks. • Prioritise less-dense areas with existing indigenous plants and seed banks for ease of recovery and provision of shade for thermoregulation of *Chlorolestes umbratus* and other species. • Use fell-remove-burn methods and reduce fire intensities. • Investigate the feasibility of partial or staggered clearing for gradual transition, especially for *C. umbratus*. 2. Maintain a diversity of vegetation types and ages to achieve greater odonate diversity.	1. Habitat requirements of invertebrates difficult to establish. Therefore restore flow regime, substrate and vegetation. Cater for habitat needs of endemic taxa. 2. Maintain and restore indigenous plant biotopes, thus facilitating the recovery of sensitive and endemic species. • Cultivate and maintain indigenous plants and seed banks. • Prioritise less-dense areas with existing indigenous plants for ease of recovery. • Use fell-remove-burn methods and reduce fire intensities.

Table 1 continued.

	Aerial Odonata	Benthic macroinvertebrates
B. PROTECT & PRIORITISE	1. Prevent invasion rather than correct the effects thereof. 2. Identify areas for protection. Protection of biodiverse areas should always be prioritised. 3. Prioritise less-dense or biodiverse areas for clearing for ease of recovery and to prevent extreme changes in shade and temperature. 4. Incorporate landscape or catchment management considerations into decisions regarding protection and prioritisation.	
Landscape considerations	Maintain longitudinal and lateral conductivity to facilitate colonisation and to prevent fragmentation and isolation.	
	• Dispersal to adjacent catchments may be possible by strong fliers (Anisoptera). Regional considerations may be necessary. • Alien trees may act as a physical barrier to movement, as may newly-cleared areas. Dispersal abilities of endemic species should be considered. • Partial clearing, 'stepping stones' or corridors of cleared areas may facilitate dispersal of Odonata to newly-cleared areas.	• Most aquatic taxa are not strong fliers and colonisation usually occurs from other areas within a single catchment. • Clearing programmes should therefore be integrated into catchment management. • Corridors of cleared areas along one side of the river only may facilitate dispersal and colonisation of new areas.
C. EVALUATE & MONITOR	1. Assessments should precede and follow clearing: - Initial assessments should identify biodiverse areas or detect invasion, thus informing prioritisation and protection decisions. - Post-clearing assessments should monitor recovery and inform future restoration techniques. 2. Use a range of taxonomic groups. 3. Investigate the use of indicators for rapid assessment of alien disturbance, taking seasonal and geographic variation into account.	
	• Species assemblages may initially be used to classify marginal plant biotopes. • Test the effectiveness of *Allocnemis leucosticta* and *Pseudagrion furcigerum* as indicator and detector species of alien disturbance. • Determine the proportion of stenotopic, endemic to widespread, eurytopic species.	• Use SASS to measure overall river health only. • Test the effectiveness of Teloganodidae and Heptageniidae as detector species. If effective, they can be used to link SASS results to alien disturbance in the Western Cape. • Assess the proportion of sensitive to tolerant families.
D. INTEGRATE	1. Formalise the process to include planning, implementation and evaluation phases. 2. Form linkages with related organisations and processes, for example, the River Health Programme (RHP), Resource Directed Measures (RDM) and Integrated Catchment Management (ICM).	